Life History Evolution in Extant and Extinct Laurasiatheria – Case Studies Elucidating the Junctions among Selective Forces, Disparity, and Trait Evolution

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Abstract

This thesis presents several case studies on life history evolution in Laurasiatheria, a diverse group of mammals occupying a wide range of habitats. The respective group in each case study was chosen based on its suitability to answer an underlying question. Additionally, one case study investigates domestication as driver for variation within a species. The first case study aims for a closer look on the Schultz's rule and heterochrony in the relative eruption sequence of the permanent dentition in lower jaws of deer, Cervidae. Cervids were chosen because of their relative uniform mandibular architecture. Schultz's rule implies that slower growing animals replace their deciduous teeth earlier in relative sequence compared to molar eruption to counterbalance tooth decay and maintain a functional tooth set during growth. The study revealed several heterochronic shifts in tooth eruption during the evolution of deer and resulted in an ancestral tooth eruption sequence, which can also be found in the fossil record. In contrast, the relative eruption sequence is not correlated with any life history variable and thus it does not provide information about the life history of cervids. The second study investigated the brain size of cave bears and compared it to extant bear species. Encephalization, or brain size in relation to body size, is linked to some life history variables in Ursidae such as gestation time, newborn mass, weaning mass, and litter size. The results suggest that cave bears had a small brain compared to body size, due to a decoupled body and brain size evolution in which the increase of body size outpaced the one of brain size. Additionally, the trade-off between fat storage and brain size as well as diet might have impacted the relative brain size of cave bears. The degree of encephalization of cave bears suggests that this species gave birth to many, light weighted cubs and had prolonged gestation; mass at weaning was small. The growth of different bear species was investigated using histological thin sections of the midshaft of femora. The growth rate of cave bears from different European localities was investigated and compared to the one of black bears, brown bears, polar bears, sloth bears, and sun bears. The bone cortex of all bear species exhibits a fibrolamellar complex and mostly varies in amounts of parallel-fibered and lamellar bone. Cave bears exhibit a high growth rate and late maturity. The altitude of the locality in which the cave bear remains were found was correlated with growth rate. The growth rate of cave bears indicates that this species gave birth to many, small offspring. In the final case study presented in this thesis, the aim was to investigate how domestication affects variation within a species. For this, the extinct Niata cattle from South America was used as case study. The Niata was a heavy brachycephalic cattle variety. It was described by Darwin and sparked debates among scientists in Europe due to its peculiar appearance. These debates are addressed in an integrative investigation of the Niata using anatomical description, geometric morphometrics, finite element analysis, and genetic analysis. The anatomical description shows clear distinctions between the Niata traits and lethal malformations with which its brachycephaly was compared. The morphometric and genetic analyses show the distinctiveness of the Niata compared to other cattle and places it close to the European taurine breeds. Additionally, the finite

element analysis revealed released stress on the Niata skull during bilateral bite. The Niata is an illustrative case on how human intervention shapes domesticated species. To summarize, the case studies presented in this thesis exemplify how bones and teeth can be used to infer life history of extant and extinct animals as well as how humans shape animals during domestication.

Keywords: heterochrony, Schultz's rule, encephalization, hibernation, palaeohistology, growth rate, domestication, chondrodysplasia

Laurasiatheria sind eine artenreiche Gruppe von Säugetieren, welche viele verschiedene Habitate bewohnen. Diese Dissertation beschäftigt sich mit Fallstudien zur Evolution der ‚life history' (Lebensgeschichte) dieser Gruppe. Die Auswahl der jeweiligen Studienobjekte in den Fallstudien basiert auf der Möglichkeit bestimmte Fragestellungen zu beantworten. Eine zusätzliche Fallstudie beschäftigt sich mit Domestikation und innerartlicher Variation. Die erste Fallstudie untersucht die Schultz' Regel und Heterochronie in der relativen Zahneruptionssequenz der permanenten Bezahnung im Unterkiefer von Hirschartigen. Die generelle Morphologie des Unterkiefers von Hirschartigen ist nicht sehr variabel, daher eignet sich dieser gut für eine vergleichende Studie. Schultz' Regel besagt, dass ein langsam wachsendes Tier die Milchzähne in relativer Sequenz zu den Molaren früher wechselt. Dies geschieht, damit der Zahnabnutzung entgegengesteuert wird und immer ein funktionsfähiges Gebiss vorhanden bleibt. Diese Fallstudie deckte mehrere Heterochronien in der Evolution von relativer Zahneruptionssequenz auf und resultierte in einer ursprünglichen Sequenz, welche auch in einem ausgestorbenen Verwandten von Hirschartigen gefunden werden konnte. Es wurden keine Korrelationen zwischen verschiedenen life history-Variablen und relativer Zahneruptionssequenz gefunden. Die zweite Fallstudie untersucht die Gehirngrösse von Höhlenbären und vergleicht diese mit der von heutigen Bärenartigen. Der Grad an Enzephalisation, also der Grad der Gehirngrösse in Relation zu Körpergrösse, korreliert mit verschiedenen life history-Variablen wie Tragzeit, Gewicht beim Abstillen, Gewicht der Neugeborenen und Anzahl von Neugeborenen. Es zeigte sich dass der Höhlenbär ein kleines Gehirn verglichen mit seiner Körpergrösse besass. Der Grund dafür ist eine überproportionale Körpergrössenzunahme in der Evolutionslinie zum Höhlenbären, wogegen die Gehirngrösse weniger stark zunahm. Des Weiteren könnte die Gehirngrösse von Nahrung und Speicherung von Fett im Körper negativ beeinflusst worden sein. Die kleine relative Gehirngrösse von Höhlenbären weist darauf hin, dass diese Tiere nach langer Tragzeit viele, kleine Junge zur Welt brachten. Zusätzlich hatten die Jungen ein leichtes Gewicht beim Abstillen. Das Wachstum von Höhlenbären wurde mithilfe von histologischen Dünnschliffen untersucht. Dafür wurde die Mitte der Diaphyse von Femora untersucht. Für diese Studie wurden Höhlenbärenreste von verschiedenen europäischen Fundorten untersucht, und mit dem Wachstum von Braunbären, Eisbären, Lippenbären, Schwarzbären und Sonnenbären verglichen. Femora von Bären zeigen einen fibrolamellaren Komplex und Variation entsteht hauptsächlich durch unterschiedliche Anteile an parallelfaserigem und lamellarem Knochen. Höhlenbären waren schnell wachsende Tiere die erst spät verwachsene Epiphysenfugen im Femur hatten. Es zeigte sich eine Korrelation zwischen Höhenlage der Fundstelle und Wachstumsrate. Die Wachstumsrate von Höhlenbären weist auf eine Reproduktionsstrategie mit vielen kleinen Jungtieren hin. Die letzte Fallstudie untersucht Domestikation und Variation in Rindern. Das Studienobjekt ist das ausgestorbene Niata Rind aus Südamerika. Diese Rindervariation hatte einen stark verkürzten Schädel. Charles Darwin war einer der ersten der dieses Tier beschrieb

und damit Diskussionen in den wissenschaftlichen Kreisen Europas entfachte. Diese Diskussionen dienen als Basis für die präsentierte Fallstudie. Das Niata Rind wird mithilfe von einer anatomischen Beschreibung, sowie Landmark-basierenden, biomechanischen und genetischen Methoden untersucht. Die Anatomie der Niata zeigt eindeutige Unterschiede zu Missbildungen, die zu ähnlichen Schädelkonfigurationen führen. Die Landmark-basierenden und genetische Daten zeigen einen klaren Unterschied zwischen der Niata und anderen Rindern und platzieren die Niata nahe zu den europäischen taurinen Rinderrassen. Zusätzlich zeigt die biomechanische Analyse, dass der Niataschädel unter geringerer Spannung steht während der Kaubewegung. Die Niata ist ein besonders auffälliges Beispiel dafür, wie Menschen das Aussehen von domestizierten Tieren beeinflussen können. Diese Dissertation zeigt auf wie Knochen und Zähne benutzt werden können um die Biologie von ausgestorbenen und rezenten Säugetieren zu rekonstruieren und wie Menschen durch Domestikation die Variabilität innerhalb von Tiergruppen beeinflussen.

Schlüsselwörter: Heterochronie, Schultz‘ Regel, Enzephalisation, Winterschlaf, Paläohistologie, Wachstumsrate, Domestikation, Chondrodysplasie

Introduction

The study of life history based on bones and teeth has contributed essential information to our knowledge of the biology of extant and extinct animals [1-4]. In mammals, a wide variety of methods can be used to infer growth, maturity, and encephalization based on skeletal remains [2, 3, 5-10]. Fast growing animals attain maturity early in life but also tend to be short lived. The opposite is true for slow growing animals [11]. Certain variables on this spectrum can be predicted by investigating the relative brain size of animals [12, 13]. Brain size can be determined by measuring the brain cavity within a skull [14].

Selection of any kind is the driver of evolution. Processes such as natural and sexual selection have led to the observed intraspecific and interspecific variation in organisms [15]. Several times independently, humans have domesticated different species of animals and plants, conducting a process of artificial selection. Taking organisms out of their original habitat changed the selective forces on them, thus leading to changes in their biology and morphology [16].

The study object – Laurasiatheria

Laurasiatheria are a disparate monophyletic group of placental mammals, which is distinct from the other major clades, which include Afrotheria, Xenarthra, and Euarchontoglires [17-20]. They are subdivided into Carnivora, Cetartiodactyla, Chiroptera, Eulipotyphla, Perissodactyla, and Pholidota (Figure 1) [20]. Based on a molecular based estimate, the split between Laurasiatheria and Euarchontoglires occurred sometime between 79 – 88 Mya ago [17]. Following Averianov and Lopatin [21], the oldest fossil record of a laurasiatherian mammal is *Gypsonictops*, an early leptictid from the Campanian/ Maastrichtian (83.6 – 72.1 Mya) of North America. In contrast, following O'Leary et al. [19], the oldest crown group member of Laurasiatheria is *Protungulatum donnae* (64.9 Mya*).* Because of the investigated species of the case studies, a more detailed introduction is given to Cervidae, Ursidae, and Bovidae, with remarks on domestication.

Cervidae are a diverse group within Artiodactyla and, at least in recent taxa, easiest distinguished by their antlers, which are bilateral bony structures based on the frontal bone. Antlers are shed annually and in most species are only produced by males [22]. The European endemic *Procervulus* from the MN3 (Neogene Mammal Zone 3, 20.5 – 18.0 Mya) [23] is considered the first true cervid [24, 25]. A considerable amount of size variation is observed within cervids. The southern Pudu, *Pudu puda*, is with 8 kg the smallest cervid today [26]. Biggest cervid species include the extant *Alces alces*, with up to 800 kg [26], as well as extinct forms such as *Megaloceros giganteus*, with about 700 kg [27]. Cervidae are one of the most successful mammalian taxa on islands and usually undergo the process of dwarfing in these secluded environments [28]. The process of dwarfing can be very fast

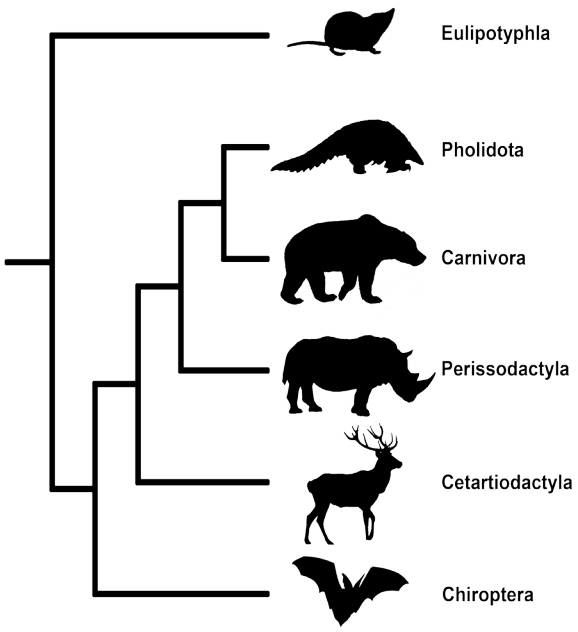

Figure 1: Phylogenetic relationships among Laurasiatheria, after Burda et al. [20].

in deer, as was exemplified in red deer from Jersey, Channel Islands [29]. A famous extinct example was *Candiacervus ropalophorus* from Crete, which reached an estimated body mass of only 59 kg [2]. Several extant smaller island subspecies of deer were described. Among those are the Svalbard reindeer, *Rangifer tarandus platyrhynchus*, and the white-tailed deer from Hunting Island, *Odocoileus virginianus venatorius* [28].

The evolutionary history of Ursidae can be traced back to the late Oligocene, with *Cephalogale*. This animal was small compared to most extant bears and its dentition indicates an omnivorous diet [30, 31]. The small and omnivorous ursid *Ursavus*, a long lasting taxon from the Miocene, gave reportedly rise to all extant bear species [30, 31]. Today, at least eight different bear species are described: the giant panda (*Ailuropoda melanoleuca*), Andean bear (*Tremarctos ornatus*), American black bear (*Ursus americanus*), brown bear (*U. arctos*), sun bear (*U. malayanus*), polar bear (*U. maritimus*), Asiatic black bear (*U. thibetanus*), and sloth bear (*U. ursinus*) [32]. The body size of these species ranges from 25 kg in small sun bears to 800 kg in large polar bears. Ecologically, bears are very diverse and inhabit the polar region as well as the tropics [32]. Most extant Ursidae are omnivorous, however, the giant panda is almost exclusively herbivorous whereas the polar bear is hypercarnivorous [33]. During the Pleistocene, Eurasia was home to one of the biggest bear species (500 kg) [34], or maybe even the biggest bear species (1500 kg) [35], the cave bear (*U. spelaeus*). This animal was dependent on caves for hibernation and thus is one of the most commonly recovered Pleistocene mammals [35, 36]. The lineage of cave bears split from the one leading to polar bear and brown bear about 2.75 and 1.4 Ma ago [37, 38]. Early on, the cave bear linage increased plant matter in its diet and many different lines of evidence suggest an almost complete herbivorous diet for *U. spelaeus* [33, 35, 39, 40].

Bovidae appear first in the fossil record in the Early Miocene with *Eotragus* [31]. Bovids are best recognizable by their horns on the frontal bone, which are permanent, living structures with a bone core and a horn sheet [22, 41]. The smallest bovid species today is the royal antelope, *Neotragus pygmaeus*, with a body weight of 1.5 kg in small adults, and the biggest one is the gaur, *Bos gaurus*, with

up to 1’200 kg [26]. Several bovid species were domesticated by humans. However, no other has provided humans with such a diverse range of exploitable resources as the domestic cattle, *B. taurus* [16]. The ancestor of the domestic cattle was the aurochs, *B. primigenius*, which appeared in Europe in the Middle Pleistocene and was hunted to extinction [16, 31]. The aurochs was domesticated at least twice independently, leading to the European taurine, or humpless, line and the Indian indicine, or humped, line [42]. Cattle was domesticated about 8’200 years ago with the first certain cattle remains coming from Turkey. During the process of domestication, cattle became smaller and several characteristics of the “domestication syndrome” are displayed [16, 43]. This syndrome suggests that an unifying, underlying embryological event is responsible for the observed similarities in behaviour, anatomy, and morphology of domesticated animals, namely a mild neural crest cell deficit [43]. However, the universality of the “domestication syndrome” was questioned [44]. In cattle, not all characteristics proposed by Wilkins et al. [43] are found. Nonetheless, during domestication cattle e.g., became tamer, decreased brain size, shortened their muzzle, changed pigmentation, and expressed floppy ears [44].

The study system – Bones and teeth

Most tissues of the body decay shortly after an organism has died. With this, a considerable amount of information about the dead organism is lost. Bones and teeth, on the other hand, are highly mineralized and withstand decay for a much greater period of time. Because of this, bones and teeth are essential to the study of archaeology and palaeontology [9, 45, 46]. Information found in the shape and size of bones can provide crucial insides into the phylogenetic position of animals as well as their variability [9, 47, 48]. Additionally, bones can reveal details about the life style of extinct animals by indicating adaptations to habitat and diet [9]. The functional morphological aspect of bones is crucial to understand how fast for example a Mesozoic marine reptile could swim [49], or how strong the bite of a *Tyrannosaurus rex* was [50]. Besides the overall shape and size, the microstructure of bones provides additional information about the life of extinct vertebrates. The histological profile of bone thin sections can be used to make predictions about speed of growth, ontogeny, phylogeny, and environment of animals [1-5, 8, 51]. Additionally, it provides insights into mechanics of the bone and thus has functional morphological implications [8]. The bones of the skull often are closely associated with sensory organs. Bone cavities such as the brain cavity or the cavity of the inner ear have become essential to the study of palaeobiology [10, 52, 53].

In vertebrate palaeontology, teeth are of particular importance. Often times, teeth are the only remains found of an extinct animal [9, 45]. In mammals, teeth are highly specialized and taxonomic indicative. In contrast to other vertebrates, most

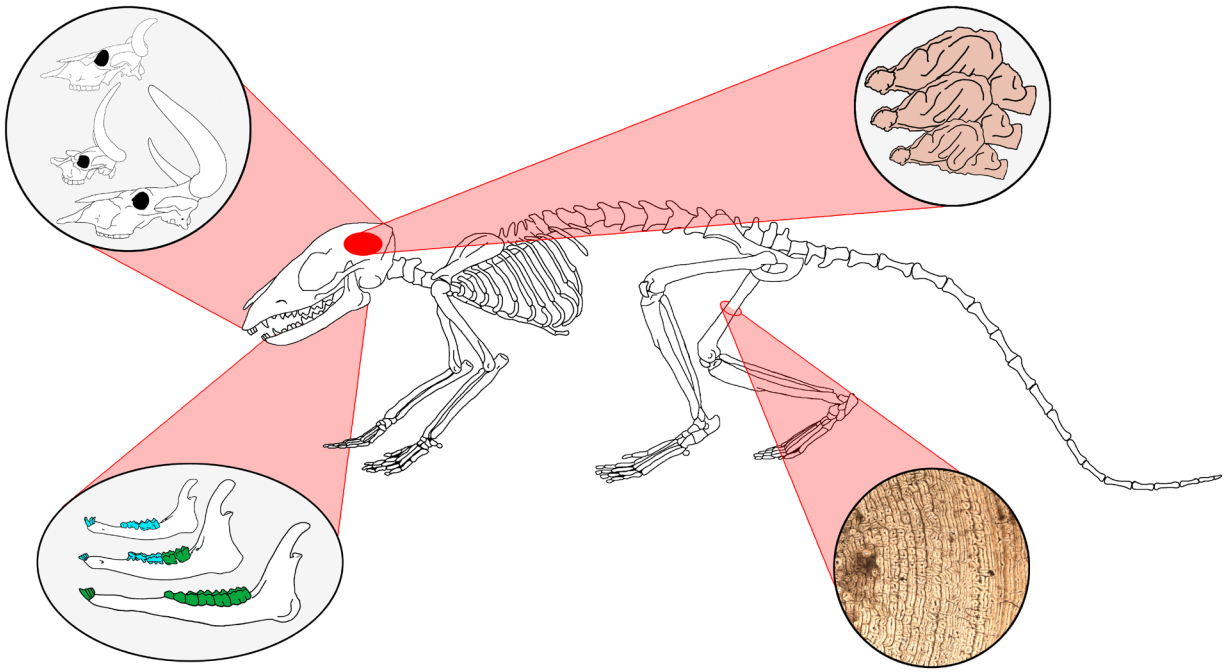

Figure 2: Overview of the focus of the four chapters of this thesis based on the generalized, schematic drawing of a mammalian skeleton (based on *Tupaia*, Gregory 1910 [60, p. 276]. The skull and teeth were generalized by removing the postorbital bar and using the placental tooth formula 3143/3143 [45]. Chapter one is indicated by a series of lower jaws with change from deciduous teeth (blue) to permanent teeth (green). Chapter two is indicated by a series of brains with different sizes and chapter three by the histology of the femur. Chapter four is indicated by cattle skulls with different sizes and shapes.

mammals only produce two generations of teeth [45]. Teeth can provide crucial information about the diet of an animal and can even provide insights into the environmental changes [54-56]. Additionally, information found in the cementum layer surrounding the roots of teeth can be used to reconstruct the absolute age of a mammal at the time of death [2, 57]. In mammals, it was also proposed that the pattern of tooth replacement can be used to infer growth speed, which is known as the Schultz's rule [58]. Nonetheless, the evidence for the Schultz's rule and its implications is not conclusive [59].

Aims and Overview

The main focus of this thesis was to use modern phylogenetic comparative, morphological comparative, and histological methods and information on skeletal remains to elucidate evolutionary processes that underpin the life history and disparity of Laurasiatheria. We used different laurasiatherian species as case studies based on their suitability to answer an underlying question (Figure 2).

The first chapter analyses the dental eruption pattern in the mandible of Cervidae, and it aims to understand the value of such patterns in reconstructing life history of extinct animals. Cervidae were chosen because of their uniform dental formula as well as their mostly similar lower jaw morphology and tooth height [45, 61]. In contrast, there is much diversity within Carnivora in the reduction of the dental

formula [45]. The idea that the relative timing of emergence of different replacement teeth compared to molar eruption is linked to speed of growth goes back to the work of A. Schultz [62, 63]. Based on this, Smith [58] proposed the Schultz's rule which should be able to tell the overall speed of growth of a species. This rule is mostly used in primatology and palaeoanthropology with some supporting the rule [64] and others disproving it [59, 65]. Although, the rule was originally also proposed for "ungulates," only few studies have investigated the applicability of this rule in Artiodactyla [66] or Perissodactyla [67, 68]. By compiling a comprehensive dataset of 719 lower jaws of 25 extinct and extant taxa, chapter one shows how the Schultz's rule is not applicable to Cervidae. The relative emergence of replacement teeth reflects the phylogenetic relatedness among different cervid species. Thus, it allows reconstructing the ancestral emergence formula for this group. Ancestral stage reconstruction based on PGi resulted in an eruption sequence of m1 – m2 – i1 – i2 – i3 – c – m3 – (ppp) at the base of the cervid tree. This formula is supported with evidence from the fossil record of Artiodactyla. Several heterochronic shifts in the emergence sequences were detected.

The second and third chapter make use of the exceptional abundance of well-preserved cave bear (*U. spelaeus* s.l.) remains in the fossil record to investigate the growth and life history of an extinct member of the Pleistocene megafauna [35, 69]. Chapter 2 investigates the absolute and relative brain size of cave bears in the context of extant and extinct Ursidae and associated life history variables. For this, the brain volume of 412 skulls of 10 ursid species were measured. Additionally, linear measurements of the same skulls were taken to estimate individual body size [70]. The expensive nature of brain tissue results in many life history and ecological trade-offs [12, 71-76]. For bears, relative brain size, the size of the brain in context of body size, is correlated with gestation time, newborn mass, weaning mass, and litter size [12]. Cave bears had a small brain size compared to body mass, which indicates that this species gave birth to many, small cubs, had a low weaning mass, and long gestation time. The small relative brain size of cave bears is the result of ecological changes and a decoupled body and brain size evolution in favour of body size.

The third chapter investigates the growth and associated life history variables of cave bears and compares it to growth in five extant and one other extinct bear species. For this, transverse histological thin sections of 77 femora were investigated. Cave bear samples stem from a wide geographical and altitudinal range within Europe and represent 23 localities. Information found in bone thin sections has proven its potential to reconstruct speed of growth as well as time of skeletal and sexual maturity [2, 3, 51, 77, 78]. The bone tissue of cave bears exhibits a fibrolamellar bone with varying degrees of order. Early ontogenetic stages and the innermost part of the bone cortex ex-

hibit more unordered woven-fibered bone whereas in older animals and in the outer cortex the more ordered parallel-fibered and lamellar bone is found. A similar histology is found in *U. arctos*, *U. americanus*, and *U. deningeri*. In contrast, the histology of *U. malayanus* and *U. maritimus* shows more parallel-fibered and lamellar bone. *U. ursinus* mostly differs from other bear species in vascularization. Cave bears reached femoral skeletal maturity late in life, with an age of about 10-13 years, and grew at a high pace. The high growth speed indicates that cave bears reached sexual maturity early in life and large litter sizes [11, 79, 80].

Chapter 4 makes use of one of humankind's biggest natural experiments, domestication [16], to study the range of intraspecific variation and their implications for evolution. For this, an extinct South American cattle variety served as case study. The Niata was the only short faced, or brachycephalic, cattle breed and found fame in the writings of Darwin on evolution [81]. To investigate the skull and lower jaw shapes of cattle with focus on the Niata, a morphospace of 316 skulls and 238 lower jaws was created. Additionally, the body size, body proportions, external suture obliteration, and basicranial angle of this cattle were investigated and compared with other breeds. SNPs data were used to analyse the genetics of the Niata and finite element models of the skulls of Niata, Zebu, and Simmentaler were created to assess the change of stress distribution in the skull during biting. The compiled evidence of all these analyses show that the Niata was a cattle breed of average size and proportions with a peculiar skull shape that was very distinct from other breeds. There was less stress on the skull of the Niata during bilateral and unilateral bite, which indicates a better adaptability to different food sources. Genetically, the Niata is distinct from other cattle breeds.

The appended abstracts and documents represent additional publications and work I was involved with that are thematically linked to the main chapters of my thesis. Appendix I is a book review for "Hypsodonty in Mammals—Evolution, Geomorphology, and the Role of Earth Surface Processes" by Richard H. Madden. In this book, the author discusses the role the environment has on the emergence of high crowned teeth in different mammalian taxa from all parts of the world. Case studies of extant goats and humans are linked with deep time evolutionary changes to the dentition of endemic South American mammals. The second appended document is the abstract of a review on bone histology in mammals by Kolb et al. [51]. In this work, I was third author because of my participation in the sampling of three extinct lagomorph species, one extinct hippopotamid species, and one extinct eulipotyphlan species. I prepared thin sections of 29 bones for this study. The aim of Kolb et al. was to summarize the literature on mammalian bone histology and add new information on some island species providing insights into the process of island evolution. Appendix III is the abstract of a further col-

laborative work. In this study, the growth trajectories and allometric slope of several domesticated species is compared with their wild ancestral species. For this, several linear measurements were taken on skulls and lower jaws. The aim of this study was to investigate the uniting and discerning characteristics of domestication on skull shape and how applicable overarching concepts such as the “domestication syndrome” are in real datasets [43, 44].

References

1. Sanchez S, Tafforeau P, Clack JA, Ahlberg PE (2016). Life history of the stem tetrapod *Acanthostega* revealed by synchrotron microtomography. Nature. 537(7620):408-11.
2. Kolb C, Scheyer TM, Lister AM, Azorit C, de Vos J, Schlingemann MA, Rössner GE, Monaghan NT, Sánchez-Villagra MR (2015). Growth in fossil and extant deer and implications for body size and life history evolution. BMC Evol Biol. 15(1):19.
3. Amson E, Kolb C, Scheyer TM, Sánchez-Villagra MR (2015). Growth and life history of Middle Miocene deer (Mammalia, Cervidae) based on bone histology. C R Palevol. 14(8):637-45.
4. Köhler M, Moyà-Solà S (2009). Physiological and life history strategies of a fossil large mammal in a resource-limited environment. PNAS. 106(48):20354-8.
5. Köhler M, Marín-Moratalla N, Jordana X, Aanes R (2012). Seasonal bone growth and physiology in endotherms shed light on dinosaur physiology. Nature. 487:358–61.
6. Köhler M, Moyà-Solà S (2004). Reduction of brain and sense organs in the fossil insular bovid *Myotragus*. Brain Behav Evol. 63(3):125-40.
7. Finarelli JA, Flynn JJ (2007). The evolution of encephalization in caniform carnivorans. Evolution. 61(7):1758-72.
8. Huttenlocker AK, Woodward HN, Hall BK (2013). The biology of bone. In: Padian K, Lamm E-T, editors. Bone histology of fossil tetrapods - advancing methods, analysis, and interpretation. Berkeley and Los Angeles: University of California Press; p. 13-34.
9. Benton MJ (2005). Vertebrate palaeontology. Oxford: Blackwell Publishing.
10. Santos E, Garcia N, Carretero JM, Arsuaga JL, Tsoukala E (2014). Endocranial traits of the Sima de los Huesos (Atapuerca, Spain) and Petralona (Chalkidiki, Greece) Middle Pleistocene ursids. Phylogenetic and biochronological implications. Ann Paleontol. 100(4):297-309.
11. Stearns SC (2008). Life history evolution: successes, limitations, and prospects. Naturwissenschaften. 87(11):476-86.
12. Finarelli JA (2010). Does encephalization correlate with life history or metabolic rate in Carnivora? Biol Lett. 6(3):350-3.
13. Weisbecker V, Goswami A (2010). Brain size, life history, and metabolism at the marsupial/placental dichotomy. PNAS. 107(37):16216-21.
14. Logan CJ, Clutton-Brock TH (2013). Validating methods for estimating endocranial volume in individual red deer (*Cervus elaphus*). Behav Processes. 92:143-6.
15. Arthur W (2011). Evolution: A developmental approach. Oxford: Wiley-Blackwell.
16. Clutton-Brock J (1999). A natural history of domesticated mammals. 2nd edition. Cambridge: Cambridge University Press.
17. Murphy WJ, Eizirik E, Johnson WE, Zhang YP, Ryder OA, O’Brien SJ (2001). Molecular phylogenetics and the origins of placental mammals. Nature. 409(6820):614-8.
18. Waddell PJ, Okada N, Hasegawa M (1999). Towards resolving the interordinal

relationships of placental mammals. Syst Biol. 48(1):1-5.

19. O'Leary MA, Bloch JI, Flynn JJ, Gaudin TJ, Giallombardo A, Giannini NP, Goldberg, Goldberg SL, Kraatz BP, Luo Z-X, Meng J, Ni X, Novacek MJ, Perini FA, Randall ZS, Rougier GW, Sargis EJ, Silcox MT, Simmons NB, Spaulding M, Velazco PM, Weksler M, Wible JR, Cirranello AL (2013). The placental mammal ancestor and the post–K-Pg radiation of placentals. Science. 339(6120):662-7.
20. Burda H, Hilken G, Zrzavý J (2016). Systematische Zoologie. 2. Auflage. Stuttgart: Verlag Eugen Ulmer (utb).
21. Averianov AO, Lopatin AV (2014). High-level systematics of placental mammals: Current status of the problem. Biol Bull. 41(9):801-16.
22. Mickoleit G (2004). Phylogenetische Systematik der Wirbeltiere. München: Dr. Friedrich Pfeil.
23. Steininger FF (1999). Chronostratigraphy, geochronology and biochronology of the Miocene "European Land Mammal Mega-Zones" (ELMMZ) and the Miocene "Mammal-Zones (MN-Zones)". In: Rössner GE, Heissig K, Alcover JA, editors. The miocene land mammals of Europe. München: Dr. Friedrich Pfeil. p. 9-24.
24. Rössner GE (1995). Odontologische und schädelanatomische Untersuchungen an *Procervulus* (Cervidae, Mammalia). Münchner Geowiss Abh A. 29
25. Groves CP (2007). Family Cervidae. In: Prothero DR, Foss SE, editors. The Evolution of Artiodactyls. Baltimore: Johns Hopkins University Press. p. 249-56.
26. MacDonald DW (2009). The Encyclopedia of Mammals. Oxford: Oxford University Press.
27. Stuart AJ (1991). Mammalian extinctions in the late Pleistocene of northern Eurasia and North America. Biol Rev. 66(4):453-562.
28. Geer A, Lyras G, Vos J, Dermitzakis M (2010). Evolution of island mammals. Adaptation and extinction of placental mammals on islands. West Sussex: Wiley-Blackwell.
29. Lister AM (1989). Rapid dwarfing of red deer on Jersey in the Last Interglacial. Nature. 342(6249):539-42.
30. McLellan B, Reiner DC (1994). A review of bear evolution. Bears. 9:85-96.
31. Agusti J, Anton M (2013). Mammoths, Sabertooths, and Hominids: 65 Million Years of Mammalian Evolution in Europe. New York: Columbia University Press.
32. Hunter L (2011). Carnivores of the world. Princeton (New Jersey): Princeton University Press.
33. van Heteren AH, MacLarnon A, Soligo C, Rae TC (2016). Functional morphology of the cave bear (*Ursus spelaeus*) mandible: a 3D geometric morphometric analysis. Org Divers Evol. 16(1):299-314.
34. Christiansen P (1999). What size were *Arctodus simus* and *Ursus spelaeus* (Carnivora: Ursidae)? Ann Zool Fenn. 36(2):93-102.
35. Rabeder G, Nagel D, Pacher M (2000). Der Höhlenbär. Stuttgart: Thorbecke Verlag.
36. Fortes GG, Grandal-d'Anglade A, Kolbe B, Fernandes D, Meleg IN, García-Vázquez A, Pinto-LIona AC, Constantin S, de Torres TJ, Ortiz JE, Frischauf C, Rabeder G, Hofreiter M, Barlow A (2016). Ancient DNA reveals differences in behaviour and sociality between brown bears and extinct cave bears. Mol Ecol. 25(19):4907-18.
37. Bon C, Caudy N, de Dieuleveult M, Fosse P, Philippe M, Maksud F, Beraud-Colomb É, Bouzaid E, Kefi R, Laugier C, Rousseau B, Casane D, van der Pflicht J, Elalouf J-M (2008). Deciphering the complete mitochondrial genome and phylogeny of the extinct cave bear in the Paleolithic painted cave of Chauvet. PNAS. 105(45):17447-52.
38. Krause J, Unger T, Noçon A, Malaspinas A-S, Kolokotronis S-O, Stiller M, Soi-

belzon L, Spriggs H, Dear PH, Briggs AW, Bray SCE, O'Brien SJ, Rabeder G, Matheus P, Cooper A, Slatkin M, Pääbo S, Hofreiter M (2008). Mitochondrial genomes reveal an explosive radiation of extinct and extant bears near the Miocene-Pliocene boundary. BMC Evol Biol. 8(1):1-12.

39. Bocherens H, Fizet M, Mariotti A (1994). Diet, physiology and ecology of fossil mammals as inferred from stable carbon and nitrogen isotope biogeochemistry: implications for Pleistocene bears. Palaeogeogr Palaeoclimatol Palaeoecol. 107(3):213-25.
40. Bocherens H (2015). Isotopic tracking of large carnivore palaeoecology in the mammoth steppe. Quat Sci Rev. 117:42-71.
41. Hall BK (2005). Bones and cartilage: developmental and evolutionary skeletal biology. London, San Diego: Elsevier Academic Press.
42. MacHugh DE, Shriver MD, Loftus RT, Cunningham P, Bradley DG (1997). Microsatellite DNA variation and the evolution, domestication and phylogeography of taurine and zebu cattle *Bos taurus* and *Bos indicus*. Genetics. 146(3):1071-86.
43. Wilkins AS, Wrangham RW, Fitch WT (2014). The "Domestication Syndrome" in mammals: a unified explanation based on neural crest cell behavior and genetics. Genetics. 197(3):795-808.
44. Sánchez-Villagra MR, Geiger M, Schneider RA (2016). The taming of the neural crest: a developmental perspective on the origins of morphological covariation in domesticated mammals. R Soc Open Sci. 3(6)
45. Thenius E (1989). Zähne und Gebiß der Säugetiere. Berlin: W. de Gruyter.
46. Hillson S (2005). Teeth. Cambridge: Cambridge University Press.
47. Schmid E (1972). Knochenatlas: für Prähistoriker, Archäologen und Quartärgeologen. Amsterdam: Elsevier Publishing.
48. Zelditch ML, Swiderski DL, Sheets HD (2012). Geometric morphometrics for biologists - a primer. 2nd edition. San Diego: Academic Press.
49. Massare JA (1988). Swimming capabilities of Mesozoic marine reptiles: implications for method of predation. Paleobiology. 14(2):187-205.
50. Bates KT, Falkingham PL (2012). Estimating maximum bite performance in *Tyrannosaurus rex* using multi-body dynamics. Biol Lett. 8:660-4.
51. Kolb C, Scheyer TM, Veitschegger K, Forasiepi AM, Amson E, Van der Geer AAE, Van den Hoek Ostende L, Hayashi S, Sánchez-Villagra MR (2015). Mammalian bone palaeohistology: a survey and new data with emphasis on island forms. PeerJ. 3:e1358.
52. Evans DC, Ridgely R, Witmer LM (2009). Endocranial anatomy of Lambeosaurine Hadrosaurids (Dinosauria: Ornithischia): a sensorineural perspective on cranial crest function. Anat Rec. 292(9):1315-37.
53. Pfaff C, Martin T, Ruf I (2015). Bony labyrinth morphometry indicates locomotor adaptations in the squirrel-related clade (Rodentia, Mammalia). Proc Biol Sci. 282(1809)
54. Mihlbachler MC, Rivals F, Solounias N, Semprebon GM (2011). Dietary change and evolution of horses in North America. Science. 331(6021):1178-81.
55. Madden RH (2015). Hypsodonty in mammals - evolution, geomorphology, and the role of earth surface processes. Cambridge: Cambridge University Press.
56. Bastl K, Semprebon G, Nagel D (2012). Lowmagnification microwear in Carnivora and dietary diversity in *Hyaenodon* (Mammalia: Hyaenodontidae) with additional information on its enamel microstructure. Palaeogeogr Palaeoclimatol Palaeoecol. 348–349:13-20.
57. Calvert W, Ramsay MA (1998). Evaluation of age determination of polar bears

by counts of cementum growth layer groups. Ursus. 10:449-53.
58. Smith HB (2000). 'Schultz's Rule' and the evolution of tooth emergence and replacement patterns in primates and ungulates. New York: Cambridge University Press.
59. Godfrey LR, Samonds KE, Wright PC, King SJ (2005). Schultz's unruly rule: dental developmental sequences and schedules in small-bodied, folivorous lemurs. Folia Primatol. 76:77-99.
60. Gregory W (1910). The orders of mammals. New York: Bulletin of the American Museum of Natural History.
61. Janis C (1988). An estimation of tooth volume and hypsodonty indices in ungulate mammals, and the correlation of these factors with dietary preference. In: Russell D, Santoro J-P, Sigogneau-Russell D, editors. Teeth revisited: proceedings of the VIIth international symposium on dental morphology. Mémoires du Muséum national d'Histoire naturelle, Science de la Terre (Série C), Tome 53. Paris: Éditions du Muséum national d'Histoire naturelle. p. 367–87.
62. Schultz AH (1956). Postembryonic age changes. Basel: Karger.
63. Schultz AH (1960). Age changes in primates and their modification in man. Oxford: Pergamon Press.
64. Henderson E (2007). Platyrrhine dental eruption sequences. Am J Phys Anthropol. 134(2):226-39.
65. Jogahara YO, Natori M (2012). Dental eruption sequence and eruption times in *Erythrocebus patas*. Primates. 53(2):193-204.
66. Jordana X, Marín-Moratalla N, Moncunill-Solé B, Bover P, Alcover JA, Köhler M (2013). First fossil evidence for the advance of replacement teeth coupled with life history evolution along an anagenetic mammalian lineage. PLoS ONE. 8(7):e70743.
67. Böhmer C, Heissig K, Rössner GE (2016). Dental eruption series and replacement pattern in Miocene *Prosantorhinus* (Rhinocerotidae) as revealed by macroscopy and x-ray: implications for ontogeny and mortality profile. J Mamm Evol. 23(3):265-79.
68. Hellmund M (2013). Odontological and osteological investigations on propalaeotheriids (Mammalia, Equidae) from the Eocene Geiseltal Fossillagerstätte (Central Germany) - a full range of extraordinary phenomena. Neues Jahrb Geol Palaontol Abh. 267(2):127 - 54.
69. Stuart AJ (2015). Late Quaternary megafaunal extinctions on the continents: a short review. Geol J. 50(3):338-63.
70. van Valkenburgh B (1990). Skeletal and dental predictors of body mass in carnivores. In: Damuth J, Macfadden BJ, editors. Body size in mammalian paleobiology: estimation and biological implications. Cambridge: Cambridge University Press. p. 181-206.
71. Navarrete A, van Schaik CP, Isler K (2011). Energetics and the evolution of human brain size. Nature. 480(7375):91-3.
72. Finarelli JA, Flynn JJ (2009). Brain-size evolution and sociality in Carnivora. PNAS. 106(23):9345-9.
73. Heldstab SA, van Schaik CP, Isler K (2016). Being fat and smart: a comparative analysis of the fat-brain trade-off in mammals. J Hum Evol. 100:25-34.
74. Taylor AB, van Schaik CP (2007). Variation in brain size and ecology in *Pongo*. J Hum Evol. 52(1):59-71.
75. Isler K, van Schaik CP (2006). Metabolic costs of brain size evolution. Biol Lett. 2(4):557-60.
76. Schuppli C, Graber SM, Isler K, van Schaik CP (2016). Life history, cognition and the evolution of complex foraging niches. J Hum Evol. 92:91-100.
77. Jordana X, Marín-Moratalla N, Moncunill-Solè B, Nacarino-Meneses C, Köhler M (2016). Ontogenetic changes in the his-

tological features of zonal bone tissue of ruminants: a quantitative approach. C R Palevol. 15(1–2):255-66.

78. Marín-Moratalla N, Jordana X, Köhler M (2013). Bone histology as an approach to providing data on certain key life history traits in mammals: Implications for conservation biology. Mamm Biol. 78(6):422-9.

79. Charnov EL (1993). Life history invariants: some explorations of symmetry in evolutionary ecology. Oxford: Oxford University Press.

80. Charnov EL (1991). Evolution of life history variation among female mammals. PNAS. 88(4):1134-7.

81. Darwin C (1845). Journal of researches into the geology and natural history of the various countries visited by H.M.S. Beagle round the world, under the Command of Capt. Fitz Roy, R.N. 2nd edition. London: John Murray.

Chapter I

Tooth eruption sequences in cervids and the effect of morphology, life history, and phylogeny

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KV designed and conceived the study, collected the data, performed the analyses, prepared the figures and tables, and wrote and reviewed the manuscript.
MRSV designed and conceived the study as well as wrote and reviewed the manuscript.

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ORIGINAL PAPER

Tooth Eruption Sequences in Cervids and the Effect of Morphology, Life History, and Phylogeny

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Abstract Tooth eruption sequences vary in a non-random way among mammalian species. Several variables have been linked to this, including tooth and jaw shape, adaptations to diet, and food processing. Likewise, changes in eruption patterns correlate with the speed of postnatal growth in some groups, the Schultz's Rule pattern. Here, the eruption pattern of the permanent dentition in lower jaws from different cervid species have been investigated to discern the effect of these factors and phylogeny as well as to reconstruct the ancestral tooth eruption sequence of cervids. In ruminants, the different patterns of emergence of permanent teeth seem to be best explained by phylogeny. The degree of hypsodonty, age of first molar eruption, and life history parameters such as longevity and age of female sexual maturity do not explain the observed sequential differences in eruption patterns. The Parsimov-based analysis for the ancestral state resulted in a tooth eruption sequence of m1 – m2 – i1 – i2 – i3 – c – m3 – (ppp) for Cervidae; a pattern recorded in *Odocoileus*, *Capreolus*, and *Hydropotes*. The eruption pattern of *Caenomeryx filholi,* from the Oligocene of Gaimersheim, is identical to the result of the Parsimov-based analysis except for the presence of a first premolar, a tooth lost in cervids.

Keywords Parsimov-based genetic inference (PGi) · Continuous analysis · Heterochrony · Schultz's Rule · Ruminantia

Introduction

Mammals replace their teeth only once during their life, possessing milk (deciduous) and adult (permanent) dentitions, but molars have only one generation (e.g., Osborn and Crompton 1973). The relative sequence of permanent tooth eruption is not fixed and varies among species (e.g., Smith 2000). Several hypotheses as to why these sequential differences occur have been postulated (e.g., Slaughter et al. 1974; Tattersall and Schwartz 1974; Simpson et al. 1990; Smith 2000; Godfrey et al. 2005). The aim of this study was to document the patterns of variation in eruption sequences in a clade of mammals and to investigate the variables associated with that variation. For this, the lower jaws of cervids were studied and compared with other members of Ruminantia. The general tooth formula in the lower jaw of cervids as well as ruminants is three incisors, one canine, three premolars, and three molars (Thenius 1989) and few species such as *Myotragus*, *Connochaetes*, or *Antidorcas* have a different dental formula (Rautenbach 1971; Attwell 1980; Jordana et al. 2013). Other shared features are an incisiviform canine followed by a diastema, selenodont tooth morphology, and two distinct sets of functional teeth (van Nievelt and Smith 2005a). Nonetheless, Ruminantia do not share the same eruption pattern (e.g., Smith 2000), which allows testing for different signals such as phylogeny and anatomy as well as ecological and life history variables. In contrast, carnivorans and primates are more variable in the arrangement of teeth within the lower jaw as well as in morphology and the expression of the two sets of teeth (Thenius 1989; van Nievelt and Smith 2005a).

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Morphological Constraints, Adaptive Evolution, and Dental Eruption Patterns

The idea that the general facial architecture could influence the pattern of dental eruption was proposed based on the study of ape and hominid remains (Simpson et al. 1990). It was assumed that the human pattern of building and replacing teeth is influenced by three major factors: the reduction of the canine tooth in males, the reduction of prognathism in the hominid lineage, and the peculiarity of the human m3 (Simpson et al. 1990). Tooth morphology and size may also affect the sequential differences in tooth eruption. Slaughter et al. (1974) investigated the eruption sequence of the postcanine teeth in Afrotheria, Carnivora, Eulipotyphla, Leptictida, and Scandentia and concluded that the sequential differences are related to the different morphology of the teeth, especially the carnassials in carnivorans. In Multituberculata, the increasing size of the lower fourth premolar is considered to be causally coupled to several changes within the eruption pattern (Greenwald 1988). Other hypotheses with a more adaptive value have also been discussed in marsupial and placental mammals. One example is the relative delay of development and eruption of certain incisor teeth in marsupials and carnivorans. A late eruption of certain incisors has been linked to suckling, as the resulting open space could allow for a longer preweaning period (Luckett and Wooley 1996; van Nievelt and Smith 2005a, b). Besides that, diet and food processing have been linked with permanent tooth eruption patterns (Godfrey et al. 2001; Dirks 2003; Guthrie and Frost 2011; Forasiepi and Sánchez-Villagra 2014).

Life History and Dental Eruption Patterns

It has been shown in primates that some life history variables such as brain mass and weaning period correlate with the age of first permanent tooth eruption (Smith 1992; Smith et al. 1994; Godfrey et al. 2001). However, not only the time but also the pattern of eruption is variable even in closely related species. To explain this, Smith (2000) postulated Schultz's Rule based on the work of Adolph Schultz (1956, 1960). According to it, an animal with a slower and longer life history has a tendency to replace deciduous teeth early in the relative sequence of tooth eruption compared to eruption of molar teeth. Therefore, Schultz's Rule would reflect the dynamics between the decay of the deciduous teeth and the possibility for the jaw to accommodate molar teeth in a slow growing mammal. Fast growing mammals would not have such physical constraints because speed of jaw growth to accommodate the molar teeth would precede the loss of functionality in the deciduous dentition. The validity of Schultz's Rule has been tested on "ungulates" and primates with a strong support found in primates and "generalized ungulates" such as Suinae but with a weaker support in more "specialized ungulates" such as Ruminantia (Smith 2000). Subsequently, several studies examined this "rule." Some argued in favor of this hypothesis based on studies on platyrhines (Henderson 2007), pantodonts (McGee and Turnbull 2010), equids (Hellmund 2013), and caprines (Jordana et al. 2013); others have found exceptions in different groups including lemurs (Godfrey et al. 2005; Schwartz et al. 2005), cercopithecines (Jogahara and Natori 2012), and tarsiids (Guthrie and Frost 2011).

Phylogeny and Dental Eruption Patterns

Dental eruption in general has shown to be a reliable marker for relatedness among species. For Multituberculata, the rotative eruption of the fourth premolar, among other characters, has been proposed as synapomorphy for this group (Greenwald 1988). In the Hyaenodontidae, the different tooth eruption patterns between North American and European species have been interpreted as indicating phylogenetic signal (Bastl et al. 2011; Bastl and Nagel 2014). Afrotheria show a common synapomorphy in the development of their dentition; in general, the relative onset of the eruption of the permanent dentition is delayed compared to Archonta and Laurasiatheria (Asher and Lehmann 2008; Asher and Olbricht 2009). This is also found in xenarthrans, where the most basal forms seem to exhibit a relative delayed eruption of permanent dentitions (Ciancio et al. 2012). In primates, several studies have focused on the importance of phylogeny as explanation for differences in the tooth eruption sequence among species (Tattersall and Schwartz 1974; Byrd 1981; Schwartz et al. 2005).

Material and Methods

Specimens

A cross-sectional sampling of different ontogenetic stages of 452 cervid lower jaws representing 15 species was examined. Additionally, 30 lower jaws of *Moschus moschiferus* as well as 19 lower jaws of two tragulid species, *Hyemoschus aquaticus* and *Tragulus kaInstitut und Museum der Univernchil*, were examined (Table 1). The maximum number of lower jaws used per species was 146 (*Cervus elaphus*) and the minimum number was three (*Elaphodus cephalophus*). Captive as well as wild-caught animals of both sexes were used. Individuals exhibiting pathological signs in the lower jaw and domestic animals were excluded. Specimens from the following institutes have been studied: MHNG, Muséum d'Histoire Naturelle de la Ville de Genève; NMB, Naturhistorisches Museum Basel; NMBE, Naturhistorisches Museum Bern; PIMUZ, Paläontologisches Institut und Museum der Universität Zürich; MfN, Museum für Naturkunde Berlin; ZMUZH, Zoologisches Museum der Universität Zürich; and ZSM, Zoologische Staatssammlung München. Further, we collected data from the literature

Table 1 Tooth eruption sequences for investigated artiodactyl species

Family	Species	n	Pattern									
Cainotheriidae	*Caenomeryx filholi* [a]	66	m1	m2	i1	i2	i3	c	m3	p2	p3	p4
Cervidae	*Axis axis*	11	m1	m2	i1	i2	i3	c	m3	p4	p3	p2
	Blastocerus dichotomus	9	m1	m2	(i1	i2	m3)	i3	c	p4	p3	p2
	Capreolus capreolus	119	m1	m2	i1	i2	i3	m3	c	p2	p3	p4
	Cervus elaphus	146	m1	m2	i1	i2	m3	i3	c	p2	p3	p4
	Cervus philisi [a]	28	m1	(i2	m2)	m3	p3	p4	p2	-	-	-
	Dama dama	49	m1	i1	m2	i2	i3	c	m3	p4	p3	p2
	Elaphodus cephalophus	3	m1	m2	m3	i1	i2	i3	c	(p	p	p)
	Eucladoceros giulii [a]	60	m1	m2	m3	(p	p	p)	-	-	-	-
	Heteroprox/*Euprox* [a]	4	m1	m2	m3	(p	p	p)	-	-	-	-
	Hippocamelus sp.	4	m1	m2	m3	i1	i2	(p3	p4	p2	i3)	c
	Hoplitomeryx [a]	11	m1	m2	m3	(p	p	p)	-	-	-	-
	Hydropotes inermis	12	m1	m2	i1	i2	i3	c	m3	p4	p3	p2
	Mazama gouazoubira	34	m1	m2	m3	i1	i2	i3	c	p4	p3	p2
	Muntiacus muntjak	14	m1	m2	m3	i1	i2	p3	p2	p4	i3	c
	Odocoileus virginianus	12	m1	m2	i1	i2	i3	c	m3	(p	p	p)
	Ozotocerus bezoarticus	13	m1	m2	m3	i1	i2	i3	c	p4	p3	p2
	Procervulus praelucidus [a]	29	m1	m2	m3	(p	p	p)	-	-	-	-
	Pseudodama s. l. *nestii* [a]	20	m1	m2	m3	(p	p	p)	-	-	-	-
	Pudu puda	12	m1	m2	m3	i1	i2	i3	c	(p	p	p)
	Rusa timorensis	5	m1	m2	i1	m3	i2	(i3	c	p4	p3	p2)
	Rusa unicolor	9	m1	m2	i1	i2	m3	i3	c	p4	p3	p2
Tragulidae	*Hyemoschus aquaticus*	5	m1	m2	m3	i1	i2	i3	c	p4	p3	p2
	Tragulus kanchil	14	m1	m2	m3	(i1	p3	p4	p2)	i2	i3	c
Moschidae	*Moschus moschiferus*	30	m1	m2	m3	p4	p3	p2	i1	i2	i3	c

Unresolved sequences are indicated in parenthesis

[a] extinct

(Supplementary Table 1) to compare and analyze the correlations among variables studied.

Additionally, the tooth eruption patterns of seven extinct taxa were investigated: *Caenomeryx filholi*, *Pseudodama* s. l. *nestii*, *Eucladoceros giulii*, *Heteroprox*/*Euprox*, *Hoplitomeryx*, *Cervus philisi,* and *Procervulus praelucidus* (Table 1). *Heteroprox*/*Euprox* cannot be distinguished by dental characters and are treated as a unit. For fossil material, the following institutes were visited: IQW, Senckenberg Forschungsstation für Quartär-Paläontologie Weimar; NMB, Naturhistorisches Museum Basel; BSPG, Bayerische Staatssammlung für Paläontologie und Geologie; and NBC, Naturalis Biodiversity Center.

Data Collection

The eruption sequence of the lower jaw was documented. Each tooth was coded as not erupted, erupting, or fully erupted/functional. Teeth that were already visible under the bone but had not begun to erupt were coded as 0. As soon as one cusp or part of the tooth had penetrated through the bone it was coded as 1 and as soon as the tooth reached the functional position it was coded as 2. Nonetheless, due to different speeds of eruption, especially for the third molar, also the status of wear of the dentition and the height above the alveoli were taken into account for the sequences. Not represented stages were reconstructed according to anterior-posterior sequence as it holds true for incisors as well as molars.

Phylogenetic Framework for Cervidae

We used a compound tree based on different sources as phylogenetic framework for the heterochronic analysis. The main arrangement is according to the phylogeny of Gilbert et al. (2006). The position of *Ozotoceros bezoarticus* follows Barbanti Duarte et al. (2008) and *Candiacervus* sp. was placed as sister taxon of the fallow deer, *Dama dama* (de Vos 1984). Most branch lengths were taken from Gilbert et al. (2006). Additional branch lengths were taken from Barbanti Duarte et al. (2008) to include

Ozotoceros bezoarticus as well as the split of the two *Odocoileus* species. The divergence age for the split between the *Muntiacus* species was taken from Hernández Fernández and Vrba (2005). Splitting age between *Candiacervus* and *Dama* was estimated at around 2.15 Ma because the ancestor of *Dama dama* separated from the ancestor of *Cervus elaphus* and *Rusa unicolor* around 4.3 Ma ago (Gilbert et al. 2006).

Heterochrony Analysis for Cervidae

The resolution of the sequences of eruption was completely resolved for 12 cervid species: *Axis axis*, *Capreolus capreolus*, *Cervus elaphus*, *Dama dama*, *Elaphodus cephalophus*, *Hydropotes inermis*, *Mazama gouazoubira*, *Muntiacus muntjak*, *Odocoileus virginianus*, *Ozotoceros bezoarticus*, *Pudu puda,* and *Rusa unicolor*. Four species were added to the analyses based on literature data: *Candiacervus* sp. (van der Geer et al. 2014), *Muntiacus reevesi* (Chapman et al. 1985), *Odocoileus hemionus* (Mosby 1960), and *Rangifer tarandus* (Miller 1972). Two different methods were used to infer the heterochronic shifts as well as the ancestral sequence of tooth eruption. One was a PGi - Parsimov-based genetic inference (Harrison and Larsson 2008). This method reconstructs sequence heterochronies as well as ancestral states by treating the whole sequence as one character and using a Parsimov-based algorithm for edit-cost optimization. The analysis was conducted using the R software (version 3.0.2) as well as the package pgi 2.0. Included in this analysis were 16 cervid species as well as the eruption of the ten teeth of the adult dentition. Eruption of premolars was coded as one single event due to the significant intraspecific variation of the eruption sequence of premolars in Cervidae. The following parameters were used to conduct eight different PGi-analyses: number of sequences per cycle: 150; number of cycles: 150; and number of sequences retained at each node: 150. The semi-exhaustive search was limited to 10,000 permutations per cycle. All eight analyses were performed independently and the shortest tree was chosen because it represents the most parsimonious scenario for heterochronic shifts. In addition to a PGi-analysis, a continuous analysis (Germain and Laurin 2009) was conducted, resulting in an ancestral sequence, heterochronic shifts, as well as a 95 % confidence interval. This analysis uses squared-change parsimony (Maddison 1991) and independent contrast (Felsenstein 1985), and it is based on a Brownian motion model. The different stages were standardized between 0 and 1 using adjusted ranks formula:

$$r_s = (r - r_{min}) \Big/ (r_{max} - r_{min})$$

(Laurin and Germain 2011). Continuous analysis was performed using Mesquite (version 3.01) (Maddison and Maddison 2011), together with the module PDAP:PDTREE (version 1.16) (Midford et al. 2011).

Life History

Ruminant life history variables collected from the literature (Pérez-Barbería and Gordon 2005; Tacutu et al. 2013) include longevity, body weight, brain weight, weaning period, and the age of sexual maturity for females (Supplementary Table 2). Information on the age of first molar eruption was taken from different sources: *Apeyceros melampus* (Roettcher and Hofmann 1970), *Alces alces* (Peterson 1955), *Antidorcas marsupialis* (Rautenbach 1971), *Antilocapra americana* (Lubinski 2001), *Bison bonasus* (Wegrzyn and Serwatka 1984), *Capra ibex* (Habermehl 1985), *Capra pyrenaica* (Vigal and Machordom 1985), *Capreolus capreolus* (Habermehl 1985), *Capricornis crispus* (Miura and Yasui 1985), *Cervus elaphus* (Habermehl 1985), *Cervus nippon* (Ohtaishi 1980), *Connochaetes taurinus* (Attwell 1980), *Dama dama* (Habermehl 1985), *Damaliscus lunatus* (Mertens 1984), *Eudorcas thomsonii* (Robinette and Archer 1971), *Giraffa camelopardalis* (Hall-Martin 1976), *Hemitragus jemlahicus* (Caughley 1965), *Hippotragus niger* (Grobler 1980), *Muntiacus reevesi* (Chapman et al. 1985), *Odocoileus hemionus* (Mosby 1960), *Odocoileus virginianus* (Severinghaus 1949), *Oryx leucoryx* (Ancrenaz and Delhomme 1997), *Ovibos moschatus* (Henrichson and Grue 1980), *Ovis ammon* (Habermehl 1985), *Ovis canadensis* (Mosby 1960), *Ovis dalli* (Hemming 1969), *Ozotoceros bezoarticus* (Bianchini and Delupi 1993), *Rangifer tarandus* (Miller 1972), *Rupicapra pyrenaica* (Pérez-Barbería and Mutuberría 1996), *Rupicapra rupicapra* (Habermehl 1985), *Saiga tatarica* (Bannikov et al. 1961), *Sylvicapra grimmia* (Wilson et al. 1984), *Syncerus caffer* (Taylor 1988), and *Tragelaphus oryx* (Jeffery and Hanks 1981).

We investigated the relationship between hypsodonty index (Janis 1988) and permanent tooth eruption sequence as well as age of first molar eruption (Supplementary Table 2). First, the age of first molar eruption in the lower jaw was tested against the other variables. Second, the tooth eruption sequences of different ruminants were sorted into six different groups as predicted by Schultz's Rule. Groups are based on relative timing between tooth replacement and molar eruption (Table 2). Kendall's tau was used to test for statistical support for the correlations. Statistical analyses were performed in PAST software (version 2.17c) (Hammer et al. 2001). Adobe Photoshop CS5 was used to create the artwork for this study.

Results

Tooth Eruption

The recorded eruption sequences are shown in Table 1. Not all relative sequences could be documented to completion. All investigated Cervidae start the eruption sequence with the first

Table 2 Grouping of the tooth eruption sequences according to the Schultz's Rule

Group	Eruption sequence										Species
1	**m1**	**m2**	**m3**	(i1	i2	i3	c	p2	p3	p4)	*Antidorcas marsupialis, Antilocapra americana, Elaphodus cephalophus, Eudorcas thomsonii, Giraffa camelopardalis, Hippotragus niger, Hyemoschus aquaticus, Mazama gouazoubira, Moschus moschiferus, Muntiacus muntjak, Muntiacus reevesi, Ozotoceros bezoarticus, Pudu puda, Saiga tatarica, Sylvicapra grimmia, Syncerus caffer*
2	**m1**	**m2**	(i1	**m3**	i2	i3	c	p2	p3	p4)	*Aepyceros melampus, Capricornis crispus, Connochaetes taurinus, Damaliscus lunatus, Rusa timorensis, Rupicapra pyrenaica, Oreamnos americanus, Oryx leucoryx, Ovibos moschatus, Ovis dalli, Tragelaphus oryx*
3	**m1**	**m2**	(i1	i2	**m3**	i3	c	p2	p3	p4)	*Capra ibex, Cervus elaphus, Rusa unicolor*
4	**m1**	**m2**	(i1	i2	i3	**m3**	c	p2	p3	p4)	*Capreolus capreolus*
5	**m1**	**m2**	(i1	i2	i3	c	**m3**	p2	p3	p4)	*Axis axis, Hydropotes inermis, Odocoileus hemionus, Odocoileus virginianus*
6	**m1**	(i1	**m2**	i2	i3	c	**m3**	p2	p3	p4)	*Candiacervus* sp., *Dama dama, Rangifer tarandus*

Molars are in bold and replacement teeth are unordered (indicated by parenthesis)

molar, and except for the genera *Muntiacus* and *Hippocamelus*, all end the sequence with the eruption of the premolar teeth. In *Hippocamelus* sp. and *Muntiacus muntjak,* as well as in ruminants *Moschus moschiferus* and *Tragulus kanchil,* the last tooth to erupt was the canine. Premolar teeth always erupted simultaneously or closely tight in timing. In all South American cervids, the molar eruption took place before the first incisors were replaced. The only exception might be *Blastocerus dichotomus*, but the relative eruption sequence of i1 – i2 – m3 could not be resolved. Other related species with the same sequence are *Candiacervus* sp. and *Dama dama* with m1 – i1 – m2 – i2 – i3 – c – m3 – p4 – p3 – p2 (van der Geer et al. 2014) as well as both *Odocoileus* species also with m1 – m2 – i1 – i2 – i3 – c – m3 – (p – p – p) (Mosby 1960). The *Odocoileus virginianus* sequence differs from the ones described by Severinghaus (1949) and Brokx (1972). Three different premolar sequences were recorded in *Capreolus capreolus* (Table 3). The relative position of the third molar is not stable; it can erupt either before the third incisor or before or after the canine. *Cervus elaphus* is the most variable species, with four different tooth eruption sequences and the only documented case where premolar eruption preceded third molar eruption in one case (Table 4). The most common sequence, however, is m1 – m2 – i1 – i2 – m3 – i3 – c – p2 – p3 – p4. The closely related *Rusa* species do not share a common replacement pattern. *Rusa unicolor* replaces the teeth in the order of m1 – m2 – i1 – i2 – m3 – i3 – c – (p4 – p3 – p2), whereas *Rusa timorensis* replaces in a different order: m1 – m2 – i1 – m3 – i2 – (i3 – c – p4 – p3 – p2). Although the final sequence could not conclusively be resolved, the third molar has accelerated its eruption before the second incisor in *Rusa timorensis*.

In addition to the cervid species, the permanent tooth eruption pattern of one moschid species and two tragulid species were documented. Most basal of these are the tragulids *Hyemoschus aquaticus* and *Tragulus kanchil*. For *Hyemoschus aquaticus*, the sequence is m1 – m2 – m3 – i1 – i2 – i3 – c – p4 – p3 – p2 and for *Tragulus kanchil*, m1 – m2 – m3 – (i1 – p3 – p4 – p2) – i2 – i3 – c. The resolution of the incisors is based on the constant anterior-posterior replacement of these teeth, a pattern that rarely changes. In these two species the permanent tooth eruption patterns differ. While in one tragulid species, *Tragulus kanchil*, the eruption of the replacement teeth is premolars before incisors (with overlap), in *Hyemoschus aquaticus* a replacement pattern from anterior to posterior can be found. In *Moschus moschiferus*, the sequence is m1 – m2 – m3 – p4 – p3 – p2 – i1 – i2 – i3 – c, comparable to the one from *Tragulus kanchil*, and not documented in any cervid species. The bovid, *Sylvicapra grimmia* has a comparable tooth eruption sequence (Wilson et al. 1984).

Heterochrony

The PGi analyses resulted in eight consensus trees of similar length (minimum tree length: 9). This overall consensus in tree length suggests a very stable analysis and a fitting use of parameters. The resulting ancestral sequence for Cervidae is m1 – m2 – i1 – i2 – i3 – c – m3 – (ppp). This sequence is still present or common in *Axis*, *Odocoileus*, *Capreolus*, *Hydropotes,* and also within the range of variation of *Cervus elaphus*. Most changes happened in the sequence of the genus *Muntiacus*. Here, the analysis resulted in an acceleration of the third molar for the genera *Muntiacus* and *Elaphodus* (Muntiacini) and also in delayed eruption of the third incisor and the canine for *Muntiacus*. The uniform tooth eruption sequence of the South American representatives in the dataset originates from an accelerated eruption of the third molar. In general, cervids accelerate the eruption of different tooth positions rather than delay eruption. Details about the heterochronic shifts in the eruption sequence of cervids in phylogeny based on PGi-analysis are depicted in Fig. 1.

The continuous method resulted in an ancestral sequence of m1 – m2 – i1 – i2– m3 – i3– c – (ppp). This sequence was

Table 3 Variation in permanent premolar tooth eruption sequence found in this study

		n	p2 - p3 - p4	p4 - p3 - p2	p3 - p2 - p4	p3 - p4 - p2	(p2 - p4) - p3
Cainotheriidae	*Caenomeryx filholi* [a]	3	2	–	1	–	–
Cervidae	*Axis axis*	1	–	1?	–	–	–
	Blastocerus dichotomus	2	–	2	–	–	–
	Capreolus capreolus	10	6	3	–	–	1
	Cervus elaphus	5	4	1	–	–	–
	Cervus philisi [a]	2	–	–	–	2	–
	Dama dama	2	–	2	–	–	–
	Hippocamelus sp.	2	–	–	–	2	–
	Hydropotes inermis	2	–	2	–	–	–
	Mazama gouazoubira	1	–	1	–	–	–
	Muntiacus muntjak	2	–	–	2	–	–
	Ozotocerus bezoarticus	2	–	2	–	–	–
	Rusa timorensis	2	–	2	–	–	–
	Rusa unicolor	1	–	1?	–	–	–
Moschidae	*Moschus moschiferus*	1	–	1	–	–	–
Tragulidae	*Hyemoschus aquaticus*	1	–	1	–	–	–
	Tragulus kanchil	1	–	–	–	1	–

[a] extinct

documented in *Cervus elaphus* as well as *Rusa timorensis*. In general, the continuous method resulted in more heterochronic shifts than the PGi-analysis. All represented species had a heterochronic shift in the second lower incisor, mostly accelerating its eruption (Fig. 2).

Life History

In the investigated ruminants the age of first molar eruption as well as the pattern of dental eruption were compared with each other as well as with life history and anatomical variables. When comparing the time of first molar eruption with the grouped tooth eruption sequences, no significant correlation was detected using Kendall's tau. Nonetheless, the trend was positive. The size of the brain was highly correlated with the age of first molar eruption but not with the emergence pattern itself. However, it showed a positive trend for both correlations. Weight showed a positive correlation with the age of first molar eruption but not with the pattern of permanent tooth emergence. Longevity was also highly correlated with the age of first molar eruption and showed a positive trend. It was not correlated with the pattern of tooth eruption. The same is true for the age of female sexual maturity and weaning period. No significant correlation was found between the hypsodonty index and the pattern of permanent tooth emergence (Table 5).

Table 4 Variation of permanent tooth emergence sequences found in this study

Cervus elaphus						
m1	m2	i1	i2	i3	c	(ppp)
				m3		
Capreolus capreolus						
m1	m2	i1	i2	i3	c	(ppp)
				m3		
Muntiacus muntjak						
m1	m2	m3	i1	i2	i3	c
					(ppp)	

Discussion

This study aimed at investigating the tooth eruption sequence in Cervidae and at demarcating impacting factors thereof. Altogether, 16 lower jaw eruption sequences of cervids were used to infer the ancestral stage of tooth eruption as well as heterochronic shifts. *Cainotherium filholi* exhibited the same relative eruption sequence of the permanent dentition as the inferred ancestral stage for cervids from the PGi-analysis.

Our analyses show that the eruption patterns in ruminants are not significantly influenced by life history variables or hypsodonty. In general, related species tend to share a common or similar eruption pattern. In cervids, the overall variability of the eruption patterns is restricted due to anatomical constraints such as the ability of the jaw to accommodate all molars and the close timing of eruption of the three premolar teeth.

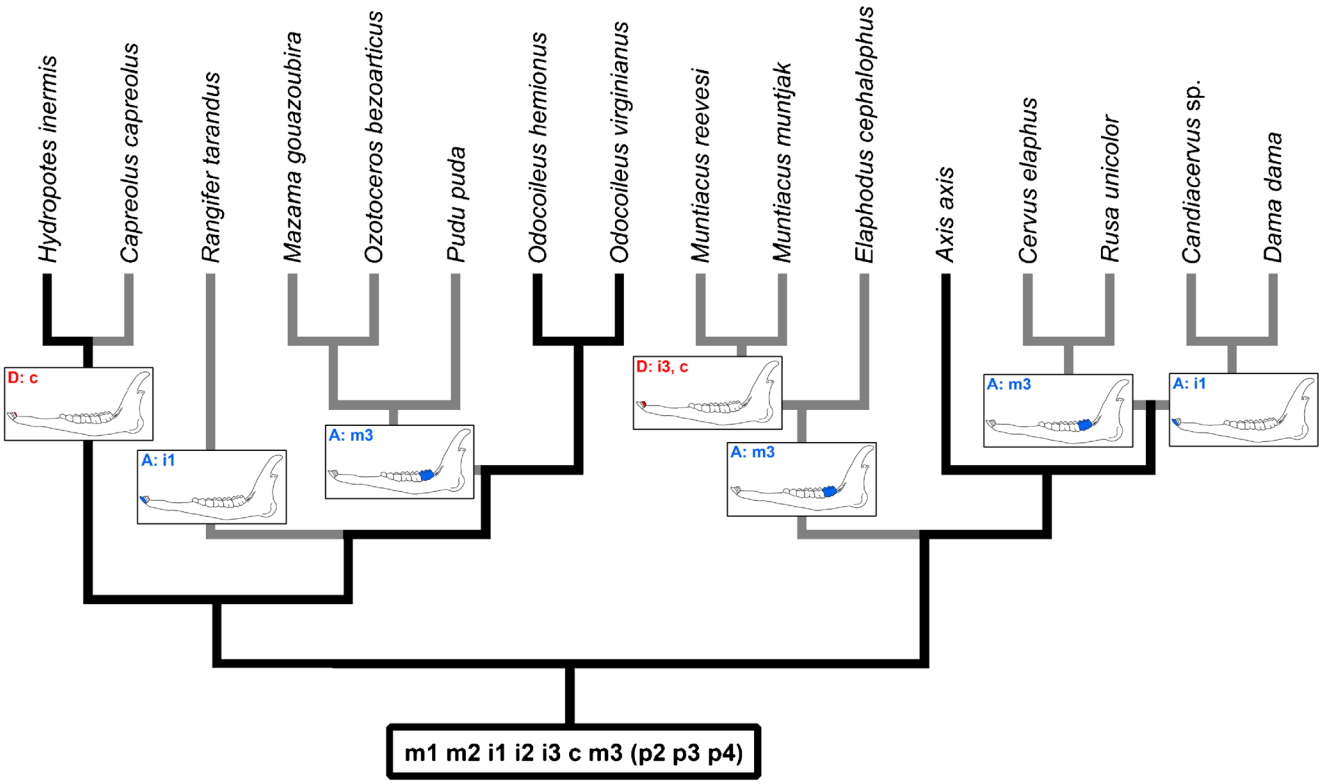


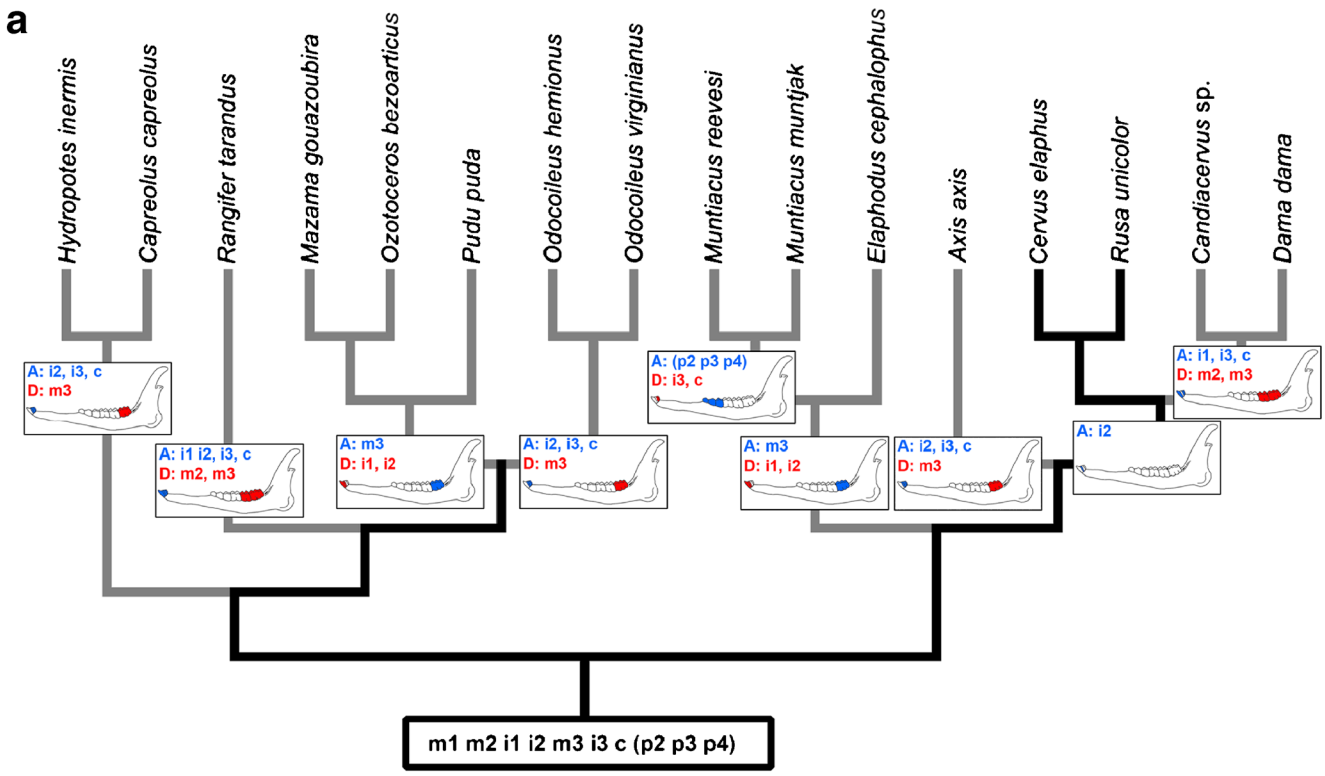
Fig. 1 Result of the sequence heterochrony analysis using PGi (Harrison and Larsson 2008). The reconstructed ancestral eruption sequence for the lower jaw is listed at the root and species and reconstructed lineages exhibiting this eruption sequence are traced in *black*. *Grey lines* indicate a change of this pattern. Lower jaws show the sequential change for a *grey line* and the affected tooth position. *red*: tooth position erupts delayed, *blue*: tooth position erupts accelerated

Sequence of Replacement

In cervids, incisors are replaced sequentially from anterior to posterior. This is also the case in all examined moschids, tragulids, *Camelus* (Bello et al. 2013), and all documented ruminants from the literature. The lower canine in Ruminantia is incisiviform and increases the size of the incisor shovel (e.g., Thenius 1989). Usually, this tooth is replaced after i3 and therefore follows the anterior-posterior sequential replacement, although eruption of i3 and canine can be closely timed (e.g., Severinghaus 1949; Habermehl 1985; Ancrenaz and Delhomme 1997). The anterior-posterior eruption sequence of the incisors and canines, however, is not generally fixed in placentals (e.g., Kirkpatrick and Sowls 1962; Matschke 1967; Smuts 1974; Habermehl 1975; Smuts et al. 1978; Shigehara 1980; Smith 2000; van Horn et al. 2003; Asher and Olbricht 2009).

The premolar teeth are replaced more or less simultaneously in cervids and any tooth could start the eruption sequence. This is supported by lower jaws where premolar height above the alveoli suggests simultaneous eruption. For *Rangifer tarandus* and *Odocoileus virginianus*, a sequence of (p2 – p3) – p4 or p2 – (p3 – p4) has been postulated (Miller 1972; Severinghaus 1949) and for *Odocoileus hemionus* a sequence of p3 – p4 – p2 (Robinette et al. 1957). Van der Geer et al. (2014) proposed a posterior-anterior replacement pattern for the premolar eruption sequence for *Candiacervus*. Habermehl (1985) documented an alternate replacement for the roe deer with p3 – p2 – p4. In Bovidae, the premolar eruption pattern is not fixed either. Nonetheless, in many species a pattern of p2 – p3 – p4 has been postulated, although for some the p2 is missing (Supplementary Table 1). Here, no case of reversed sequence has been reported but alternate eruption, either (p3 – p4) – p2 (Mosby 1960; Hemming 1969; Vigal and Machordom 1985) or p3 – (p2 – p4) (Caughley 1965). It has been widely accepted that ruminants share a sequential pattern (p2 – p3 – p4 or p4 – p3 – p2) of replacing teeth usually in the order of p2 – p3 – p4 (Osborn 1970; Smith 2000; Luo et al. 2004), but data presented here show that premolar eruption sequence can vary even in closely related species or within a species. This is also true in other placentals, although premolar eruption might not be as closely timed as in cervids (Slaughter et al. 1974; Tattersall and Schwartz 1974; Smith 1994, 2000; Gingerich and Smith 2010).

Molar eruption in cervids occurs in all recorded cases from anterior to posterior, with no exception. No evidence from other placentals has been found to contradict this (e.g., Slaughter et al. 1974; Habermehl 1985; Smith 2000).



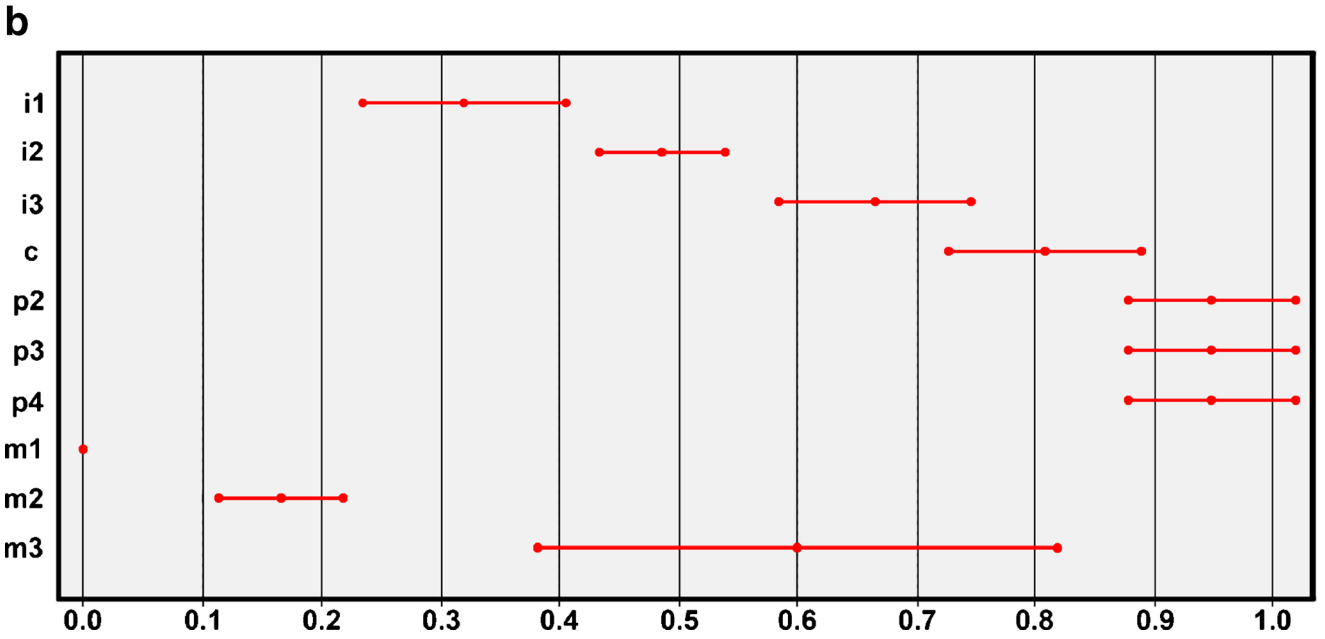


Fig. 2 Result of the sequence heterochrony analysis using continuous analysis (Germain and Laurin 2009). **a** The reconstructed ancestral eruption sequence for the lower jaw is listed at the root and species and reconstructed lineages exhibiting this eruption sequence are traced in *black*. *Grey lines* indicate a heterochronic shift in this pattern. Lower jaws indicate the sequential change for a line and the affected tooth position. *red*: tooth position erupts delayed, *blue*: tooth position erupts accelerated. **b** 95 % confidence intervals for every single tooth position. The ancestral eruption sequence is represented as midpoint and with extreme points the 95 % confidence intervals are shown

On the Methods of Sequence Heterochrony Analysis

We found differences in the results between PGi-analysis and continuous analysis, as was the case in several other studies (Geiger et al. 2014; Koyabu et al. 2014; Sheil et al. 2014). This is due to the different approach both methods have. PGi-analysis is not based on a time tree and it can deal with ties or simultaneous events in the dataset (Harrison and Larsson

Table 5 P-values from Kendall's tau for different life history traits as well as for hypsodonty index

		m1	Longevity	Brain mass	Body mass	Sexual maturity (f)	Weaning period	Hypsodonty index
m1	*p*-value:	–	0.005*	0.001*	<0.001*	<0.001*	0.007*	0.325
	tau:	–	0.347	0.466	0.513	0.412	0.363	0.132
Emergence	*p*-value:	0.186	0.393	0.093	0.053	0.115	0.427	0.318
Pattern	tau:	0.185	0.098	0.221	0.219	0.183	0.102	−0.129

It was tested for the time of first molar eruption (months) as well as for the emergence pattern itself grouped according to Table 2

2008). On the other hand, the continuous analysis incorporates branch length data and can be biased due to unresolved sequences (Germain and Laurin 2009; Koyabu et al. 2014). The transformation of the data can also be a source of bias as transformed data have the same intervals between events (Germain and Laurin 2009). Both methods differ in dealing with independence in the dataset. PGi-analysis does not assume independence between events (Harrison and Larsson 2008); continuous analysis, on the other hand, does (Germain and Laurin 2009). In general, the continuous analysis resulted in more heterochronic shifts than the PGi-analysis. Nonetheless, the 95 % confidence interval of the continuous analysis supports the result of the PGi-analysis.

Morphological Constraints, Adaption, and Dental Eruption Patterns

Simpson et al. (1990) hypothesized that the pattern of eruption of permanent dentition can be influenced by the anatomy of the upper or lower jaw. Certain anatomical constraints are also part of Schultz's Rule (Smith 2000). Cervids and bovids share a very similar dentary shape as well as tooth formula with the four anterior incisiviform teeth followed by a diastema and afterwards three premolars and three molars (e.g., Thenius 1989). Nonetheless, they do not all share the same pattern of tooth replacement. Whereas, e.g., *Dama dama* and *Candiacervus* start to replace their first incisor already early, *Pudu puda* and *Mazama gouazoubira* replace this tooth after the eruption of all three molars. The stable pattern in the cheek-dentition in cervids, where premolar teeth nearly always erupt after the third molar, indicates that replacement occurs as soon as the mandible is big enough to accommodate the whole permanent dentition. This holds also for *Hyemoschus aquaticus*, *Tragulus kanchil*, and *Moschus moschiferus*. In rare cases (once in *Cervus elaphus*), the premolar eruption precedes third molar eruption. Only a few Ruminantia such as *Ovis ammon* (Habermehl 1985) and *Myotragus balearicus* (Jordana et al. 2013) change the relative sequence between premolar eruption and the third molar one completely.

A simple but effective way to account for the effect of morphology in the ruminant dentition is the hypsodonty index (Janis 1988). Ruminant teeth share general tooth morphology; all are selenodont (e.g., Thenius 1989; Hillson 2005). Not all teeth, however, have the same height and therefore not all teeth need the same space within the jaw. Using Kendall's tau to analyze the relation between the pattern of tooth emergence and the age of first molar eruption did not result in a correlation between these parameters (Table 5). Although the size of the crown height is definitely different among the species examined, it did not lead to a change in relative eruption sequence. High crowned species such as *Antidorcas marsupialis* or *Eudorcas thomsonii* have the same eruption sequence as the low crowned *Hyemoschus aquaticus* or *Elaphodus cephalophus*. Hypsodonty does not influence the relative emergence pattern of the permanent dentition in ruminants.

Tooth Eruption as Indicator for Life History Traits

The time of eruption of the first molar was positively correlated with longevity, age of female sexual maturity, brain mass, weaning period, and body mass. For primates and "ungulates, " positive correlations among some of these traits have also been found, although not always significant (e.g., Smith 1989, 1992, 2000; Godfrey et al. 2001, 2005; Guthrie and Frost 2011). A link among different life history traits in general has been found in Artiodactyla. Brain size, for example, is correlated with body mass, and body mass again is correlated with maximum longevity (Isler and van Schaik 2012). Body size in a broad sense can be a predictor for the pace of life history. However, it might not be the source of differences (e.g., Western 1979; Read and Harvey 1989). Therefore, the age of first molar eruption can be seen as a predictor for the pace of life history in the investigated ruminants. The pattern of eruption is not linked to these life history and anatomical traits (Table 5). Schultz's Rule fails to predict the life history of Ruminantia in this case. An outstanding example in this regard is the emergence sequence of the two taxa *Muntiacus* and *Giraffa*. Both genera share the same tooth eruption pattern, but all life history variables investigated differ considerably. For example, the age of first molar eruption is 10 months in *Giraffa camelopardalis* but only 0.23 months in *Muntiacus reevesi* (Supplementary Table 2).

Phylogeny and Dental Eruption Patterns

The tooth eruption sequence in cervids, as in other mammals, is largely conserved in phylogeny (e.g., Byrd 1981; Greenwald 1988; Luo et al. 2004; Asher and Lehmann 2008; Ciancio et al. 2012), as for example seen in the genera *Capreolus* and *Hydropotes* as well as *Muntiacus* and *Elaphodus*. The divergence splits of both groups have been estimated with around 7.3 Ma for Muntiacini and 5.6 Ma for Capreolini (Gilbert et al. 2006). Nonetheless, *Capreolus* still shows the eruption sequence of *Hydropotes* within its variability, and within Muntiacini, the eruption pattern of *Elaphodus cephalophus* falls within the range of variation of *Muntiacus muntjak* (Table 4). Other examined taxa also have similar eruption sequences such as *Pudu puda*, *Mazama gouazoubira, and Ozotoceros bezoarticus; Dama dama* and *Candiacervus* sp.; as well as *Rusa unicolor* and *Cervus elaphus* (Table 1). The genus *Odocoileus* is more variable than is recorded in this study. Patterns from literature differ from the pattern observed here. *Odocoileus virginianus* for example has been documented with the same tooth eruption sequence as *Rangifer tarandus* (Severinghaus 1949; Miller 1972).

In Bovidae, some closely related species have similar sequences such as *Ovibos* and *Capricornis* as well as *Eudorcas* and *Antidorcas* (Supplementary Table 1). The emergence patterns of bovids in general, however, are less well resolved and many species exhibit unique eruption patterns. An explanation for this might be that the taxa represented are usually not closely related, having divergence times of more than 5 – 10 Ma (Bibi 2013).

Comparisons with Fossil Artiodactyls

One extinct taxon studied preserved a complete permanent eruption pattern in the lower jaw, the caenotherid *Caenomeryx filholi*, from the Oligocene of Gaimersheim (Fig. 3). Cainotheriidae are a sister taxon to ruminants (Theodor 2010). The sequence represented in this artiodactyl is in concordance with the result of the PGi-analysis (Fig. 1). Lower first premolars have been lost in modern ruminants (Thenius 1989). *Caenomeryx filholi* still possesses the complete ancestral tooth formula 3143/3143 of placental mammals (Thenius 1989) and therefore preservation of ancestral characteristics in replacement order of permanent teeth is possible.

All examined fossils from extinct taxa in this study have a constant pattern in premolar-molar eruption. This persistence of premolar eruption after molar eruption stands in contrast to Schultz's Rule, because body size range, a proxy for life history, among these species is large (e.g., Western 1979; Read and Harvey 1989).

From the literature, the ruminant *Myotragus balearicus* follows Schultz's Rule scenario (Jordana et al. 2013). This extinct island bovid has an eruption sequence of m1 – i1 – m2 – (p3 – p4) – m3 and the first molar emerged at around nine months (Jordana et al. 2013). It is one of the rare cases where premolar eruption accelerated the third molar one and studies showed that this species had a slow life history as well as a long life span (Marín-Moratalla et al. 2011; Jordana et al. 2012, 2013). The next living relative to the genus *Myotragus,* however, is the genus *Ovis* (Lalueza-Fox et al. 2005). *Ovis ammon* also accelerates premolar eruption before the third molar one (Habermehl 1985). Therefore, the eruption pattern of *Myotragus* might be influenced by phylogeny as well.

Conclusion

Tooth eruption in cervids, as commonly in extant Ruminantia, shows that there is variation in the permanent tooth eruption sequences even among closely related species. According to our results, these sequential differences are not influenced by brain size, body mass, hypsodonty, or the life history factors tested for but rather by their phylogeny. Closely related species often share their tooth eruption sequences and differences in patterns can be explained by observed intraspecific and interspecific variations. These results stand in contrast to the proposed Schultz's Rule-hypothesis because here, the speed of growth should have had a bigger impact on the permanent tooth eruption sequence than any other factor (Smith 2000). Nonetheless, Smith (2000) stated that the predictions of this rule are not as strong for ruminant artiodactyls, which she included in so called "specialized ungulates." These "ungulates" would only slowly adapt to changes in pace of life history.

The age of first molar eruption, however, was correlated with life history variables such as longevity, age of female sexual maturity, and weaning period. Both brain weight and weight in general were highly correlated with age of first molar eruption. This agrees with the literature on primates as well as "ungulates" (e.g., Smith 1989, 2000; Smith et al. 1994; Godfrey et al. 2001, 2005; Guthrie and Frost 2011). The fossil record as well as heterochrony methods allow for reconstruction of the ancestral emergence pattern. A pattern of m1 – m2

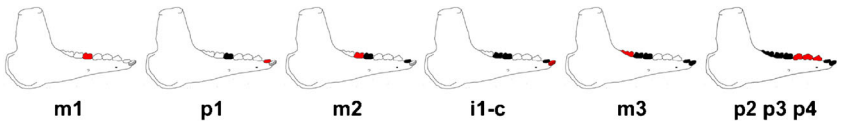


Fig. 3 Documented tooth eruption sequence for the lower jaw of *Caenomeryx filholi*. Newly erupted teeth (*red*), previously erupted ones (*black*)

–i1 – i2 – i3 – c – m3 – (ppp) holds true for the common ancestor of today's cervids, based on results from PGi-analysis, as well as for *Caenomeryx filholi*.

Premolar eruption remains unresolved due to the variability of relative eruption sequence in these teeth. Sequential as well as alternate replacement was documented even within one species, which makes phylogenetic statements based on premolar replacement problematic.

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References

Ancrenaz M, Delhomme A (1997) Teeth eruption as a means of age determination in captive Arabian oryx, *Oryx leucoryx* (Bovidae, Hippotraginae). Mammalia 61:135–138. doi: 10.1515/mamm.1997.61.1.109

Asher RJ, Lehmann T (2008) Dental eruption in afrotherian mammals. BMC Biol 6:1–11. doi:10.1186/1741-7007-6-14

Asher RJ, Olbricht G (2009) Dental ontogeny in *Macroscelides proboscideus* (Afrotheria) and *Erinaceus europaeus* (Lipotyphla). J Mammal Evol 16:99–115. doi: 10.1007/s10914-009-9105-2

Attwell CAM (1980) Age determination of the blue wildebeest *Connochaetes taurinus* in Zululand. S Afr J Zool 15:121–130

Bannikov AG, Zhirnov LV, Lebedeva LS, Fandeev AA (1961) Biologiya saigaka [Biology of the Saiga Antelope]. Selskokhozyaistvennaya Literatura, Moscow

Barbanti Duarte JM, González S, Maldonado JE (2008) The surprising evolutionary history of South American deer. Mol Phylogenet Evol 49:17–22. doi: 10.1016/j.ympev.2008.07.009

Bastl K, Nagel D (2014) First evidence of the tooth eruption sequence of the upper jaw in *Hyaenodon* (Hyaenodontidae, Mammalia) and new information on the ontogenetic development of its dentition. Palaeontol Z 88:481–494. doi: 10.1007/s12542-013-0207-z

Bastl K, Morlo M, Nagel D, Heizmann E (2011) Differences in the tooth eruption sequence in *Hyaenodon* ('Creodonta': Mammalia) and implications for the systematics of the genus. J Vertebr Paleontol 31: 181–192. doi: 10.1080/02724634.2011.540052

Bello A, Sonfada ML, Umar AA, Umaru MA, Shehu SA, Hena SA, Onu JE, Fatima OO (2013). Age estimation of camel in Nigeria using rostral dentition. Sci J Anim Sci 2:9–14

Bianchini JJ, Delupi LH (1993) Determinación de la edad en ciervos de las pampas (*Odocoileus bezoarticus*) mediante el estudio comparado del desarrollo y desgaste de los dientes. PHYSIS (Buenos Aires), Secc. C, 48:27–40

Bibi F (2013) A multi-calibrated mitochondrial phylogeny of extant Bovidae (Artiodactyla, Ruminantia) and the importance of the fossil record to systematics. BMC Evol Biol 13:166. doi: 10.1186/1471-2148-13-166

Brokx PA (1972) Age determination of Venezuelan White-Tailed deer. J Wildl Manage 36:1060–1067. doi: 10.2307/3799233

Byrd KE (1981) Sequences of dental ontogeny and callitrichid taxonomy. Primates 22:103–118. doi: 10.1007/BF02382561

Caughley G (1965) Horn rings and tooth eruption as criteria of age in the Himalayan thar, *Hemitragus jemlahicus*. New Zealand J Sci 8:333–351

Chapman DI, Chapman NG, Colles CM (1985). Tooth eruption in Reeves' muntjac (*Muntiacus reevesi*) and its use as a method of age estimates (Mammalia: Cervidae). J Zool 205:205–221. doi: 10.1111/j.1469-7998.1985.tb03529.x

Ciancio MR, Castro MC, Galliari FC, Carlini AA, Asher RJ (2012) Evolutionary implications of dental eruption in *Dasypus* (Xenarthra). J Mammal Evol 19:1–8. doi: 10.1007/s10914-011-9177-7

de Vos J (1984) The Endemic Pleistocene Deer of Crete. North-Holland Publishing Company, Amsterdam

Dirks W (2003) Effect of diet on dental development in four species of catarrhine primates. Am J Primatol 61:29–40. doi: 10.1002/ajp.10106

Felsenstein J (1985) Phylogenies and the comparative method. Am Nat 125:1–15

Forasiepi AM, Sánchez-Villagra MR (2014) Heterochrony, dental ontogenetic diversity, and the circumvention of constraints in marsupial mammals and extinct relatives. Paleobiology 40:222–237. doi: 10.1666/13034

Geiger M, Forasiepi AM, Koyabu D, Sánchez-Villagra MR (2014) Heterochrony and post-natal growth in mammals—an examination of growth plates in limbs. J Evol Biol 27:98–115. doi: 10.1111/jeb.12279

Germain D, Laurin M (2009) Evolution of ossification sequences in salamanders and urodele origins assessed through event-pairing and new methods. Evol Dev 11:170–190. doi: 10.1111/j.1525-142X.2009.00318.x.

Gilbert C, Ropiquet A, Hassanin A (2006) Mitochondrial and nuclear phylogenies of Cervidae (Mammalia, Ruminantia): systematics, morphology, and biogeography. Mol Phylogenet Evol 40:101–117. doi:10.1016/j.ympev.2006.02.017

Gingerich PD, Smith BH (2010) Premolar development and eruption in the early Eocene adapoids *Cantius ralstoni* and *Cantius abditus* (Mammalia, Primates). Contrib Mus Paleontol Univ Mich 32:41–47

Godfrey LR, Samonds KE, Jungers WL, Sutherland MR (2001) Teeth, brains and primate life histories. Am J Phys Anthropol 114:192–214. doi: 10.1002/1096-8644(200103)114:3<192::AID-AJPA1020>3.0.CO;2-Q

Godfrey LR, Samonds KE, Wright PC, King SJ (2005) Schultz's unruly rule: dental development sequences and schedules in small-bodied, folivorous lemurs. Folia Primatol 76:77–99. doi: 10.1159/000083615

Greenwald NS (1988) Patterns of tooth eruption and replacement in multituberculate mammals. J Vertebr Paleontol 8:265–277. doi: 10.1080/02724634.1988.10011709

Grobler JH (1980) Body growth and age determination of the sable *Hippotragus niger niger* (Harris, 1838). Koedoe 23:131–156. doi: 10.4102/koedoe.v23i1.641

Guthrie EH, Frost FR (2011) Pattern and pace of dental eruption in *Tarsius*. Am J Phys Anthropol 145:446–451. doi: 10.1002/ajpa.21525

Habermehl K-H (1975) Altersbestimmung bei Haus- und Labortieren, 2nd edn. Verlag Paul Parey, Hamburg

Habermehl K-H (1985) Altersbestimmung bei Wild- und Pelztieren – Möglichkeiten und Methoden – ein praktischer Leitfaden für Jäger, Biologen und Tierärzte, 2nd edn. Verlag Paul Parey, Hamburg

Hall-Martin AJ (1976) Dentition and age determination of the giraffe *Giraffa camelopardalis*. J Zool 180:263–289. doi: 10.1111/j.1469-7998.1976.tb04678.x

Hammer Ø, Harper DAT, Ryan PD (2001) PAST: Paleontological statistics software package for education and data analysis. Palaeontol Electron 4:9 pp

Harrison LB, Larsson HC (2008) Estimating evolution of temporal sequence changes: a practical approach to inferring ancestral developmental sequences and sequence heterochrony. Syst Biol 57:378–387. doi: 10.1080/10635150802164421

Hellmund M (2013) Odontological and osteological investigations on propalaeotheriids (Mammalia, Equidae) from the Eocene Geiseltal Fossillagerstätte (Central Germany)—a full range of extraordinary phenomena. Neues Jahrb Geol P-A 267:127–154. doi: 10.1127/0077-7749/2013/0300

Hemming JE (1969) Cemental deposition, tooth succession, and horn development as criteria of age in Dall sheep. J Wildl Manage 33: 552–558. doi: 10.2307/3799377

Henderson E (2007) Platyrrhine dental eruption sequences. Am J Phys Anthropol 134:226–239. doi: 10.1002/ajpa.20658

Henrichson P, Grue H (1980) Age criteria in the muskox (*Ovibos moschatus*) from Greenland. Danish Rev Game Biol 11:3–18

Hernández Fernández M, Vrba ES (2005) A complete estimate of the phylogenetic relationships in Ruminantia: a dated species-level supertree of the extant ruminants. Biol Rev 80:269–302. doi: 10.1017/S1464793104006670

Hillson S (2005) Teeth, 2nd edn. Cambridge Manuals in Archaeology. Cambridge University Press, New York

Isler K, van Schaik CP (2012) Allomaternal care, life history and brain size evolution in mammals. J Hum Evol 63:52–63. doi:10.1016/j.jhevol.2012.03.009

Janis CM (1988) An estimation of tooth volume and hypsodonty indices in ungulate mammals, and the correlation of these factors with dietary preference. In: Russell DE, Santoro J-P, Sigogneau-Russell D (eds) Teeth Revisited: Proceedings of the VIIth International Symposium on Dental Morphology. Mémoires du Muséum national d'Histoire naturelle, Science de la Terre (Série C), Tome 53, Éditions du Muséum national d'Histoire naturelle, Paris, pp 367–387

Jeffery RCV, Hanks J (1981) Age determination of eland *Taurotragus oryx* (Pallas, 1766) in the Natal highveld. S Afr J Zool 16:113–122

Jogahara YO, Natori M (2012) Dental eruption sequence and eruption times in *Erythrocebus pata*. Primates 53:193–204. doi: 10.1007/s10329-011-0286-y

Jordana X, Marín-Moratalla N, DeMiguel D, Kaiser TM, Köhler M (2012) Evidence of correlated evolution of hypsodonty and exceptional longevity in endemic insular mammals. Proc Roy Soc B 279: 3339–3346. doi: 10.1098/rspb.2012.0689

Jordana X, Marín-Moratalla N, Moncunill-Solé B, Bover P, Alcover JA, Köhler M (2013) First fossil evidence for the advance of replacement teeth coupled with life history evolution along an anagenetic mammalian lineage. PLoS ONE 8(7): e70743. doi: 10.1371/journal.pone.0070743

Kerr MA, Roth HH (1970) Studies on the agricultural utilization of semi-domesticated eland (*Taurotragus oryx*) in Rhodesia. Rhod J Agr Res 8:149–155

Kirkpatrick RD, Sowls LK (1962) Age determination of the collared peccary by the tooth-replacement pattern. J Wildl Manage 26:214–217. doi: 10.2307/3798608

Koyabu D, Werneburg I, Morimoto M, Zollikofer CPE, Forasiepi AM, Endo H, Kimura J, Ohdachi SD, Truong Son N, Sánchez-Villagra MR (2014) Mammalian skull heterochrony reveals modular evolution and a link between cranial development and brain size. Nat Commun 5:3625. doi:10.1038/ncomms4625

Lalueza-Fox C, Castresana J, Sampietro L, Marquès-Bonet T, Alcover JA, Bertranpetit J (2005) Molecular dating of caprines using ancient DNA sequences of *Myotragus balearicus*, an extinct endemic Balearic mammal. BMC Evol Biol 5:70. doi:10.1186/1471-2148-5-70

Laurin M, Germain D (2011) Developmental characters in phylogenetic inference and their absolute timing information. Syst Biol 60:630–644. doi: 10.1093/sysbio/syr024

Lubinski PM (2001) Estimating age and season of death of pronghorn antelope (*Antilocapra americana* Ord) by means of tooth eruption and wear. Int J Osteoarchaeol 11:218–230. doi: 10.1002/oa.536

Luckett WP, Wooley PA (1996) Ontogeny and homology of the dentition in dasyurid marsupials: development in *Sminthopsis virginiae*. J Mammal Evol 3:327–364. doi: 10.1007/BF02077449

Luo Z-X, Kielan-Jaworowska Z, Cifelli RL (2004) Evolution of dental replacement in mammals. Bull Carnegie Mus Nat Hist 36:159–175. doi: 10.2992/0145-9058(2004)36[159:EODRIM]2.0.CO;2

Maddison WP (1991) Squared-change parsimony reconstructions of ancestral states for continuous-valued characters on a phylogenetic tree. Syst Zool 40:304–314. doi: 10.2307/2992324

Maddison WP, Maddison DR (2011) Mesquite: a modular system for evolutionary analysis. Version 3.01

Marín-Moratalla N, Jordana X, García-Martínez R, Köhler M (2011) Tracing the evolution of fitness components in fossil bovids under different selective regimes. CR Palevol 10:469–478. doi: 10.1016/j.crpv.2011.03.007

Matschke GH (1967) Aging European wild hogs by dentition. J Wildl Manage 31:109–113. doi: 10.2307/3798365

McGee EM, Turnbull WD (2010) A paleopopulation of *Coryphodon lobatus* (Mammalia: Pantodonta) from Deardorff hill Coryphodon quarry, Piceance Creek Basin, Colorado. Fieldiana Geol 52:1–12. doi: 10.3158/0096-2651-52.1.1

Mertens H (1984) Détermination de l'âge chez le topi (*Damaliscus korrigum* Ogilby) au Parc National des Virunga (Zaïre). Mammalia 48:425–435. doi: 10.1515/mamm.1984.48.3.425

Midford PE, Garland T Jr, Maddison WP (2011) PDAP Package of Mesquite. Version 1.16

Miller FL (1972) Eruption and attrition of mandibular teeth in barren-ground caribou. J Wildl Manage 36:606–612. doi: 10.2307/3799093

Miura S, Yasui K (1985) Validity of tooth eruption-wear patterns as age criteria in the Japanese serow, *Capricornis crispus*. J Mammal Soc Jpn 10:169–178. doi: 10.11238/jmammsocjapan1952.10.169

Mosby HS (1960) Manual of Game Investigational Techniques. The Wildlife Society, Ann Arbor

Ohtaishi N (1980) Estimation of sex, age, and season of death using mandibles of *Cervus nippon* excavated from an archaeological site. Arch Nat Sci 13:51–74 **(in Japanese)**.

Osborn JW (1970) New approach to Zahnreihen. Nature 225:343–346. doi: 10.1038/225343a0

Osborn JW, Crompton AW (1973) The evolution of mammalian from reptilian dentitions. Breviora 399:1–18

Pérez-Barbería FJ, Gordon IJ (2005) Gregariousness increases brain size in ungulates. Oecologia 145:41–52. doi: 10.1007/s00442-005-0067-7

Pérez-Barbería FJ, Mutuberría G (1996) Teeth eruption pattern in Cantabrian chamois *Rupicapra pyrenaica parva*. Acta Theriol 41: 217–221

Peterson RL (1955) North American Moose. University of Toronto Press, Toronto

Rautenbach IL (1971) Ageing criteria in the springbok, *Antidorcas marsupialis* (Zimmermann, 1780) (Artiodactyla: Bovidae). Ann Transv Mus 27:83–133

Read AF, Harvey PH (1989) Life history differences among the eutherian radiations. J Zool 219:329–353. doi: 10.1111/j.1469-7998.1989.tb02584.x

Robinette WL, Archer AL (1971) Notes on ageing criteria and reproduction of Thomson's gazelle. E Afr Wildl J 9:83–98. doi: 10.1111/j.1365-2028.1971.tb00222.x

Robinette WL, Jones DA, Rogers G, Gashwiler JS (1957) Notes on tooth development and wear for Rocky Mountain mule deer. J Wildl Manage 21:134–153. doi: 10.2307/3797579

Roettcher D, Hofmann RR (1970) The ageing of impala from a population in the Kenya Rift Valley. E Afr Wildl J 8:37–42. doi: 10.1111/j.1365-2028.1970.tb00828.x

Schultz AH (1956) Postembryonic age changes. In: Hofer H, Schultz AH, Starck D (eds) Primatologia, 1st vol. Karger, Basel, pp 887–964

Schultz AH (1960) Age changes in primates and their modification in man. In: Tanner JM (ed) Human Growth, 3rd vol. Pergamon Press, Oxford, pp 1–20

Schwartz GT, Mahoney P, Godfrey LR, Cuozzo FP, Jungers WL, Randria GFN (2005) Dental development in *Megaladapis edwardsi* (Primates, Lemuriformes): implications for understanding life history variation in subfossil lemurs. J Hum Evol 49:702–721. doi: 10.1016/j.jhevol.2005.08.006

Severinghaus CW (1949) Tooth development and wear as criteria of age in white-tailed deer. J Wildl Manage 13:195–216. doi: 10.2307/3796089

Sheil CA, Jorgensen M, Tulenko F, Harrington S (2014) Variation in timing of ossification affects inferred heterochrony of cranial bones in Lissamphibia. Evol Dev 16:292–305. doi: 10.1111/ede.12092

Shigehara N (1980) Epiphyseal union, tooth eruption, and sexual maturation in the common tree shrew, with reference to its systematic problem. Primates 21:1–19. doi: 10.1007/BF02383820

Simpson SW, Lovejoy CO, Meindl RS (1990) Hominoid dental maturation. J Hum Evol 19:285–297. doi: 10.1016/0047-2484(90)90070-R

Slaughter BH, Ronald PH, Nobuko EP (1974) Eruption of cheek teeth in Insectivora and Carnivora. J Mammal 55:115–125. doi: 10.2307/1379261

Smith BH (1989) Dental development as a measure of life history in primates. Evolution 43:683–688. doi: 10.2307/2409073

Smith BH (1992) Life history and the evolution of human maturation. Evol Anthropol 1:134–142. doi: 10.1002/evan.1360010406

Smith BH (1994) Sequence of emergence of the permanent teeth in *Macaca*, *Pan*, *Homo*, and *Australopithecus*: its evolutionary significance. Am J Hum Biol 6:61–76. doi: 10.1002/ajhb.1310060110

Smith BH (2000) 'Schulz's rule' and the evolution of tooth emergence and replacement patterns in primates and ungulates. In: Teaford MF, Smith MM, Ferguson MWJ (eds) Development, Function and Evolution of Teeth. Cambridge University Press, Cambridge, pp 212–228

Smith BH, Crummet TL, Bradt KL (1994) Ages of eruption of primate teeth: a compendium for aging individuals and comparing life histories. Yearb Phys Anthropol 37:177–231. doi: 10.1002/ajpa.1330370608

Smuts GL (1974) Age determination in Burchell's zebra (*Equus burchelli antiquorum*) from the Kruger National Park. S Afr J Wildl Res 4:103–115

Smuts GL, Anderson JL, Austin JC (1978) Age determination of the African lion (*Panthera leo*). J Zool 185:115–146. doi: 10.1111/j.1469-7998.1978.tb03317.x

Tacutu R, Craig T, Budovsky A, Wuttke D, Lehmann G, Taranukha D, Costa J, Fraifeld VE, de Magalhaes JP (2013) Human ageing genomic resources: integrated databases and tools for the biology and genetics of ageing. Nucleic Acids Res 41(D1):D1027-D1033. doi: 10.1093/nar/gks1155

Tattersall I, Schwartz JH (1974) Craniodental morphology and the systematics of the Malagasy lemurs (Primates, Prosimii). Anthropol Pap Am Mus 52:139–192

Taylor RD (1988) Age determination of the African buffalo, *Syncerus caffer* (Sparrman) in Zimbabwe. Afr J Ecol 26:207–220. doi: 10.1111/j.1365-2028.1988.tb00972.x

Thenius E (1989) Zähne und Gebiß der Säugetiere. In: Niethammer J, Schliemann H, Starck D (eds) Handbuch der Zoologie, VIII Mammalia. Walter de Gruyer, Berlin

Theodor JM (2010) Micro–computed tomographic scanning of the ear region of *Cainotherium*: character analysis and implications. J Vertebr Paleontol 30:236–243. doi: 10.1080/02724630903415979

van der Geer AAE, Lyras GA, MacPhee RDE, Lomolino M, Drinia H (2014) Mortality in a predator-free insular environment: the dwarf deer of Crete. Am Mus Novitates 3807:1–26. doi: 10.1206/3807.1

van Horn RC, McElhinny TL, Holekamp KE (2003) Age estimation and dispersal in the spotted Hyena (*Crocuta crocuta*). J Mammal 84:1019–1030

van Nievelt AFH, Smith KK (2005a) To replace or not to replace: the significance of reduced functional tooth replacement in marsupial and placental mammals. Paleobiology 31:324-346. doi: 10.1666/0094-8373(2005)031[0324:TRONTR]2.0.CO;2

van Nievelt AFH, Smith KK (2005b) Tooth eruption in *Monodelphis domestica* and its significance for phylogeny and natural history. J Mammal 86:333-341. doi: 10.1644/BWG-224.1

Vigal CR, Machordom A (1985) Tooth eruption and replacement in the Spanish wild goat. Acta Theriol 19:305-320

Wegrzyn M, Serwatka S (1984) Teeth eruption in the European bison. Acta Theriol 29:111-121.

Western D (1979) Size, life history and ecology in mammals. Afr J Ecol 17:185-204. doi: 10.1111/j.1365-2028.1979.tb00256.x

Wilson VJ, Schmidt JL, Hanks J (1984) Age determination and body growth of the common duiker *Sylvicapra grimmia* (Mammalia). J Zool 202:283-297. doi: 10.1111/j.1469-7998.1984.tb05955.x

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Supplementary Table 1
Eruption sequences of Ruminantia reported in the literature considered in this work.

Family	Genus	Eruption Sequence										Source
Antilocapridae	*Antilocapra americana*	m1	m2	m3	i1	p3	p4	i2	p2	i3	c	Lubinski 2001
Bovidae	*Aepyceros melampus*	m1	m2	i1	m3	(i2	p2	p3)	i3	c	p4	Roettcher and Hofmann 1970
	Antidorcas marsupialis	m1	m2	m3	i1	i2	i3	c	p3	p4	-	Rautenbach 1971
	Bison bonasus	m1	m2	i1	(p2	m3)	p3	i2	i3	p4	c	Wegrzyn and Serwatka 1984
	Capra ibex	m1	m2	i1	(i2	p	p	p	m3)	i3	c	Habermehl 1985
	Capra pyrenaica	m1	m2	i1	(p3	p4	m3)	i2	p2	i3	c	Vigal and Machordom 1985
	Capricornis crispus	m1	m2	i1	m3	i2	p2	p3	p4	i3	c	Miura and Yasui 1985
	Connochaetes taurinus	m1	m2	i1	m3	i2	(p3	p4)	i3	c	-	Attwell 1980
	Damaliscus lunatus	m1	m2	i1	m3	p2	i2	p3	i3	(c	p4)	Mertens 1984
	Eudorcas thomsonii	m1	m2	m3	i1	i2	i3	c	p2	p3	p4	Robinette and Archer 1971
	Hemitragus jemlahicus	m1	m2	i1	(m3	i2)	p3	(p2	p4)	i3	c	Caughley 1965
	Hippotragus niger	m1	m2	m3	i1	i2	i3	(c	p3	p2	p4)	Grobler 1980
	Oreamnos americanus	m1	m2	i1	m3	(p3	p4)	(i2	p2)	i3	c	Mosby 1960
	Oryx leucoryx	m1	m2	i1	m3	i2	p2	(i3	c)	p3	p4	Ancrenaz and Delhomme 1997
	Ovibos moschatus	m1	m2	i1	m3	i2	(p2	p3)	p4	i3	c	Henrichson and Grue 1980
	Ovis ammon	m1	m2	i1	(i2	p2	p3	p4)	(i3	m3)	c	Habermehl 1985
	Ovis dalli	m1	m2	i1	m3	(i2	p3	p4)	p2	i3	c	Hemming 1969
	Rupicapra pyrenaica	m1	m2	i1	m3	(i2	p2	p3	p4)	i3	c	Pérez-Barbería and Mutuberría 1996
	Rupicapra rupicapra	m1	(i1	m2)	(i2	p2	p3	p4	m3)	i3	c	Habermehl 1985
	Saiga tatarica	m1	m2	m3	i1	(p2	p3	p4)	i2	i3	c	Bannikov et al. 1961
	Sylvicapra grimmia	m1	m2	m3	(p2	p3	p4)	(i1	i2	i3)	c	Wilson et al. 1984
	Syncerus caffer	m1	m2	m3	i1	p2	p3	i2	p4	i3	c	Taylor 1988
	Tragelaphus oryx	m1	m2	i1	m3	i2	i3	c	(p2	p3)	p4	Kerr and Roth 1970 Jeffery and Hanks 1981
Cervidae	*Alces alces*	m1	m2	i1	(i2	p3	p4	p2	m3)	i3	c	Peterson 1955
	Candiacervus sp. †	m1	i1	m2	i2	i3	c	m3	p4	p3	p2	van der Geer et al. 2014
	Capreolus capreolus	m1	m2	i1	i2	i3	(c	m3)	p3	p2	p4	Habermehl 1985
	Cervus elaphus	m1	m2	i1	i2	i3	c	m3	(p	p	p)	Habermehl 1985
	Cervus nippon	m1	m2	i1	i2	(i3	c	m3)	(p	p	p)	Ohtaishi 1980

	Dama dama	m1	i1	i2	m2	i3	c	(m3	p	p	p)	Habermehl, 1985
	Muntiacus reevesi	m1	m2	m3	i1	i2	(p3	p2	p4)	(i3	c)	Chapman et al. 1985
	Odocoileus hemionus	m1	(m2	i1)	i2	i3	c	m3	p3	p4	p2	Robinette et al. 1957
	Odocoileus hemionus	m1	m2	i1	i2	i3	c	m3	(p	p	p)	Mosby 1960
	Odocoileus virginianus	m1	i1	m2	i2	i3	c	m3	p2	(p3	p4)	Severinghaus 1949
	Odocoileus virginianus	m1	m2	i1	(i2	m3)	i3	c	(p	p	p)	Brokx 1972
	Ozotoceros bezoarticus	m1	m2	m3	i1	i2	i3	c	(p	p	p)	Bianchini and Delupi 1993
	Rangifer tarandus	m1	i1	m2	i2	i3	c	m3	(p	p	p)	Miller 1972
Giraffidae	*Giraffa camelopardalis*	m1	m2	m3	i1	i2	(p4	p3	p2)	i3	C	Hall-Martin 1976

Tooth eruption sequences in cervids and the effect of morphology, life history, and phylogeny. Journal of Mammalian Evolution. Veitschegger K*, Sánchez-Villagra MR

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Supplementary Table 2
Life history variables and hypsodonty index for examined species. Weight, age of female sexual maturity, longevity, and weaning period from Perez-Barberia and Gordon (2005), brain size from Tacutu et al. (2013), and hypsodonty index from Janis (1988). Age of first molar eruption taken from individual literature (2.5). *Ovis canadensis* was not used in statistical analyses.

Family	Species	Weight (grams)	Age of female sexual maturity (days)	Longevity (years)	Age of M1 eruption (months)	Brain size (grams)	Weaning period (days)	Hypsodonty Index
Antilocapridae	*Antilocapra americana*	46'100	547	15.5	1.82	156	91	4.61
Bovidae	*Aepyceros melampus*	52'500	456	25.6	4.5	161	167	4.89
	Antidorcas marsupialis	39'000	213	19.8	0.93	138	121	4.89
	Bison bonasus	610'000	730	26.4	6.5	-	213	6.12
	Capra ibex	82'500	797	20.9	5	-	274	4.71
	Capra pyrenaica	57'500	548	15.2	3	-	-	-
	Capricornis crispus	80'000	1095	24	5.5	147	-	-
	Connochaetes taurinus	164'500	411	24.3	5.5	423	278	4.94
	Damaliscus lunatus	110'000	639	23.6	7	364	-	5.1
	Eudorcas thomsonii	25'000	365	20	2	76	102	3.77
	Hemitragus jemlahicus	35'200	547	21.8	2.5	-	151	4.95
	Hippotragus niger	225'000	768	22.2	6	427	213	3.77
	Oreamnos americanus	90'000	912	20.8	-	-	122	2.76
	Oryx leucoryx	121'350	794	20.8	2.8	-	137	-
	Ovibos moschatus	315'000	1096	27.4	6	-	213	3.69
	Ovis ammon	160'000	403	16.8	5	110	135	-
	Ovis canadensis	70'275	707	20.6	6	-	152	4.11
	Ovis dalli	73'100	684	19.6	1	-	129	-
	Philantomba monticola	6'250	487	15.9	-	36	-	-
	Rupicapra pyrenaica	30'000	-	12.3	3	-	-	-
	Rupicapra rupicapra	37'500	674	17.6	4.5	137	76	4.19
	Saiga tatarica	37'500	331	10.5	1	124	87	5.29

	Sylvicapra grimmia	18'500	255	15.4	2	87	191	2.97
	Syncerus caffer	700'000	1475	29.8	3.5	653	289	3
	Tragelaphus oryx	500'000	589	26.1	7	578	182	2.91
Cervidae	*Alces alces*	386'000	751	18.4	2.8	540	100	1.34
	Axis axis	36'000	766	20.8	-	134	122	-
	Candiacervus sp. †	59'000	-	18	-	-	-	-
	Capreolus capreolus	21'667	413	17.5	3.5	122	89	1.49
	Cervus elaphus	200'000	852	31.5	4.5	386	156	1.96
	Cervus nippon	42'000	500	26.3	4	108	172	2.79
	Dama dama	70'000	487	21.1	5	243	183	2.01
	Elaphodus cephalophus	33'500	639	22.7	-	80	-	1.69
	Hydropotes inermis	11'500	183	13.9	-	63	-	1.84
	Mazama gouazoubira	17'000	395	14.8	-	60	-	-
	Muntiacus muntjak	21'000	272	18.8	-	116	61	1.81
	Muntiacus reevesi	18'000	274	23.2	0.23	57	-	1.12
	Odocoileus hemionus	57'000	478	22	2.5	231	132	1.59
	Odocoileus virginianus	87'000	309	23	2.33	230	129	1.23
	Ozotoceros bezoarticus	32'500	365	21.9	0.58	121	167	2.12
	Pudu puda	10'000	274	18.3	-	-	61	1.62
	Rangifer tarandus	101'250	662	21.8	3	303	120	1.52
	Rusa timorensis	63'000	464	21.1	-	187	228	-
	Rusa unicolor	185'000	650	26.4	-	358	213	2.2
Giraffidae	*Giraffa camelopardalis*	800'000	1278	39.5	10	773	152	1.2
Moschidae	*Moschus moschiferus*	10'000	473	13.9	-	50	106	1.98
Tragulidae	*Hyemoschus aquaticus*	11'000	403	-	-	-	180	1.3

CHAPTER II

The effect of body size evolution and ecology on encephalization in cave bears and extant relatives

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The effect of body size evolution and ecology on encephalization in cave bears and extant relatives

Kristof Veitschegger

Abstract

Background: The evolution of larger brain volumes relative to body size in Mammalia is the subject of an extensive amount of research. Early on palaeontologists were interested in the brain of cave bears, *Ursus spelaeus*, and described its morphology and size. However, until now, it was not possible to compare the absolute or relative brain size in a phylogenetic context due to the lack of an established phylogeny, comparative material, and phylogenetic comparative methods. In recent years, many tools for comparing traits within phylogenies were developed and the phylogenetic position of cave bears was resolved based on nuclear as well as mtDNA.

Results: Cave bears exhibit significantly lower encephalization compared to their contemporary relatives and intraspecific brain mass variation remained rather small. Encephalization was correlated with the combined dormancy-diet score. Body size evolution was a main driver in the degree of encephalization in cave bears as it increased in a much higher pace than brain size. In *Ursus spelaeus*, brain and body size increase over time albeit differently paced. This rate pattern is different in the highest encephalized bear species within the dataset, *Ursus malayanus*. The brain size in this species increased while body size heavily decreased compared to its ancestral stage.

Conclusions: Early on in the evolution of cave bears encephalization decreased making it one of the least encephalized bear species compared to extant and extinct members of Ursidae. The results give reason to suspect that as herbivorous animals, cave bears might have exhibited a physiological buffer strategy to survive the strong seasonality of their environment. Thus, brain size was probably affected by the negative trade-off with adipose tissue as well as diet. The decrease of relative brain size in the herbivorous *Ursus spelaeus* is the result of a considerable increase in body size possibly in combination with environmental conditions forcing them to rest during winters.

Keywords: Physiological buffer, Dormancy, Diet, *Ailuropoda*, *Helarctos*, *Melursus*, *Tremarctos*, *Ursus*

Background

Cave bears, *Ursus spelaeus*, were a common faunal element during the Pleistocene of Europe and Asia [1]. The habitat of *U. spelaeus* was Eurasia with an east-west extension ranging from Spain to the Altai Region of Russia [1–3]. The ancestral species of *U. spelaeus*, *U. deningeri*, was even more widespread, with a habitat ranging from Spain to Siberia and even reaching the British Isles [1, 3–5]. At the end of the Pleistocene, cave bears shared the same fate as most other elements of the Pleistocene megafauna and became extinct [6–8]. Their time of extinction was proposed to be around 27.800–25.000 years BP [9, 10]. Based on molecular data, the sister group to cave bears are brown bears, *U. arctos*, and polar bears, *U. maritimus*, together (Fig. 2). The evolutionary lineage of *U. spelaeus* split from these two bear species sometime between 2.75 to 1.2 Ma years ago [11–13]. Traditionally, cave bears were considered to be predominantly or exclusively herbivorous based on the morphology of their teeth and jaws [1, 14–18]. Several studies presented isotopic as well as morphometric evidence confirming this hypothesis [2, 19–25]. However, the predominantly herbivorous diet of cave bears was questioned based on isotopic [26, 27], morphometric [28, 29], microwear [30, 31], and taphonomic evidence [32]. In recent years, many of these studies were dismissed based

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on methodological errors or repeated with the result that cave bears were indeed herbivorous [2, 19, 20, 33].

Cave bear brains are among the earliest ones of an extinct species to be investigated and several studies discuss different aspects of its evolution [34–42]. Many of these studies focus on the external morphology of artificial, fossil, or virtual endocasts [34, 35, 39–41]. Conflicting statements were presented concerning the overall size of the cave bear brain. Some authors suggested a small brain size compared to body size and speculated that the increase of skull size in the evolution of *U. spelaeus* outpaced brain size [35, 36]. Others suggested high brain volumes for cave bears and an opposite scenario with brain size outpacing body size [37, 38, 42]. Many factors affect the size of brains. Brain tissue itself is known to be expensive to produce and maintain [43–45]. Absolute as well as relative brain size can be influenced by social structure [46–48], environment [48–52], sensory systems [53], evolutionary history [54–57], body size evolution [42], and different physiological as well as life history trade-offs [43, 52, 57–66].

Diet can have a profound effect on brain size as was exemplified in bats and primates [67]. Recently, it was even suggested that diet had a bigger effect on brain size than sociality in primates [68]. The diet of bears is diverse with varying amounts of plant and animal matter within and among species [2]. It ranges from hypercarnivorous in polar bears, *U. maritimus*, to folivorous in giant pandas, *Ailuropoda melanoleuca* [2, 69]. Thus, diet of bears might exhibit a link to brain size.

Some bear species survive the cold seasons with extended resting periods, whereas especially tropical species are active year-round [69]. Resting periods in bears are different from deep hibernation as movement still can occur [70]. Thus, these periods are better described as dormancy in bears. Previous to dormancy, bears increase the amount of stored body fat [70]. The storage of high amounts of adipose tissue was linked to a decreased brain size [60]. Bears represent a good study object to investigate the effect of dormancy on brain size because some species are active year round whereas others increase the amount of adipose tissue annually [69].

In this study, I investigate the absolute and relative brain size of *U. spelaeus* and all extant bear species in a phylogenetic context and add remarks on *U. deningeri*. For this, I created a comprehensive brain size dataset for all extant bear species and cave bears. Additionally, I examine potential variables which could introduce energetic constraints affecting brain size evolution such as dormancy, diet, and body size. These variables were chosen because they can be reconstructed for cave bears with some measure of certainty.

Methods

Data collection

Altogether, I measured 412 skulls of 10 extant and extinct bear species (Table 1). *U. spelaeus* samples cover a time period of about 20.000 years based on radiocarbon dating [9]. Brain volume was measured using the glass bead method [71]. I used 6 mm diameter soda lime glass beads. The individual body mass (g) was inferred using the basicranial length (SKL) as described by van Valkenburgh: body mass (kg) = 2.02*Log10(SKL)-2.80 (least squares regression) [72]. Brain volume was converted into brain mass (g) using the specific weight of brain substance 1.036

Table 1 Results of body mass (g) and brain mass (g) estimates as well as residuals and investigated ecological scores

Species	n	average body mass (g)	StD body mass (g)	average body mass literature (g)	average brain mass (g)	StD brainmass (g)	average residuals	StD average residuals	diet score	dormancy score	d*d
Ailuropoda melanoleuca	5	118'637 (105'324–135'094)	10,748.36	97'500 (70'000–125'000)	281.79 (238.28–331.52)	33.89	−0.0029	0.0548	1.000	3.000	3.000
Tremarctos ornatus	8	80'918 (64'223–110'621)	15,049.56	117'500 (60'000–175,000)	227.92 (176.12–279.72)	31.33	0.0373	0.0320	1.814	3.000	5.443
Ursus americanus	28	117'116 (83'885–155'600)	20,168.42	170'000 (40'000–300'000)	256.78 (186.48–352.24)	38.39	−0.0373	0.0422	1.884	1.000	1.884
Ursus arctos	93	177'628 (92'655–320'042)	40,696.57	390'000 (55'000–725'000)	378.08 (207.20–538.72)	61.38	−0.0080	0.0464	1.637	1.000	1.637
Ursus deningeri	1	254,996	-	-	341.88	-	−0.1770	-	-	-	-
Ursus malayanus	50	82'379 (56'333–108'841)	13,709.85	52'500 (25'000–80'000)	340.43 (227.92–435.12)	47.31	0.2047	0.0403	2.684	3.000	8.051
Ursus maritimus	82	211'265 (144'141–277'270)	33,275.87	402'500 (150'000–655'000)	498.80 (393.68–611.24)	53.75	0.0525	0.0320	2.970	2.000	5.940
Ursus spelaeus	99	322'764 (209'553–425'411)	57,207.28	362'500 (225'000–500'000)	430.10 (321.16–569.80)	52.36	−0.1550	0.0443	1.000	1.000	1.000
Ursus thibetanus	29	113'424 (78'533–166'402)	21,401.65	120'000 (40'000–200'000)	282.58 (186.48–414.40)	45.66	0.0155	0.0577	1.920	1.000	1.920
Ursus ursinus	17	147'081 (124'439–183'291)	18,122.18	100'000 (50'000–150'000)	292.52 (248.64–352.24)	26.04	−0.0573	0.0360	2.606	3.000	7.818

(g/cm3) [73]. The collected data is presented in Additional file 1: Table S1. To assess the validity of previously published cranial volumes of cave bears, I additionally created a data subset predicting endocranial volume based on external skull measurements for *U. spelaeus*, *U. arctos*, and *U. malayanus* [74]. Raw data for this analysis can be found in Additional file 2: Table S2.

The materials examined in this study are from the following collections: Biologiezentrum Linz (BZL), Geology School of Aristotle University Thessaloniki (AUTH), Institut für Paläontologie Wien (PIUW), Naturalis Biodiversity Center Leiden (NBC), Naturhistorisches Museum der Burgergemeinde Bern (NMBE). Naturhistorisches Museum Wien (NHM), Naturmuseum St. Gallen (NMSG), Naturmuseum Südtirol Bozen (PZO), Muséum National d'Histoire Naturelle Paris (MNHN), Museum für Naturkunde Berlin (MfN), Paleontological Institute and Museum University of Zurich (PIMUZ), and Zoological Museum University of Zurich (ZMUZH).

Data analyses

Data were log10-transformed and examined using ordinary least squares (OLS) and phylogenetic generalized least squares (PGLS) (Fig. 1, Additional file 3: Supplementary Information). I used OLS to investigate the differences in intercepts and slopes between species. Residuals from a PGLS based on brain/body mass (g) were used to investigate the differences in relative brain size. With this, the data were corrected for the effect of size. An initial investigation revealed that the data were heavily skewed by *U. malayanus* and *U. spelaeus* because of the uneven sampling (Additional file 3: Supplementary Information). All other bear species were more similar in body mass (g)/brain mass (g). This was supported by the multiple and adjusted R^2 (Additional file 3: Supplementary Information). Thus, the basis for brain/body mass (g) residuals was the slope (0.78069) and intercept (−1.50995) as retrieved by a PGLS excluding *U. malayanus* and *U. spelaeus*. For PGLS, the species-averaged brain mass and body mass were used. Analyses were performed in R, version 3.2.3 [75]. PGLS was executed as implemented in the packages ape and caper [76, 77]. Results from OLS regressions on all data points as well as a PGLS regression with all species are presented in the Additional file 3: Supplementary Information.

The phylogenetic relationships among Ursidae is not completely understood as there are clear discrepancies between trees based on nuclear and mitochondrial DNA (mtDNA), mirroring a complex evolutionary history with introgression and incomplete lineage sorting [78]. Complete phylogenies of Ursidae including cave bears are based on mtDNA [11, 12], therefore, I use mtDNA topology as basis for the phylogenetic analyses. The relationship between cave bears and brown bear as well as polar bear was also confirmed by nuclear DNA [79]. Recently, several new, former unrecognized species and subspecies of *U. spelaeus* were described based on morphological and genetic data [3, 80–83]. However, some of these taxa are polyphyletic [84, 85]. Here, I include all these proposed cave bear species and subspecies in *U. spelaeus*, but exclude the well-established ancestral species *U. deningeri* [17]. *U. deningeri* is considered an anagenetic ancestor to *U. spelaeus* [1, 80] and thus was excluded from all analyses as it would either represent a duplication or cannot be properly placed in phylogeny. Branch lengths for phylogenetically informed analyses were retrieved from Nyakatura and Bininda-Emonds [86] and Bon [12].

Due to uneven sampling and small sample sizes in species-averaged datasets, I use non-parametric analyses. A Kruskal-Wallis test followed by a Dunn's test with Bonferroni adjustment was used on the resulting

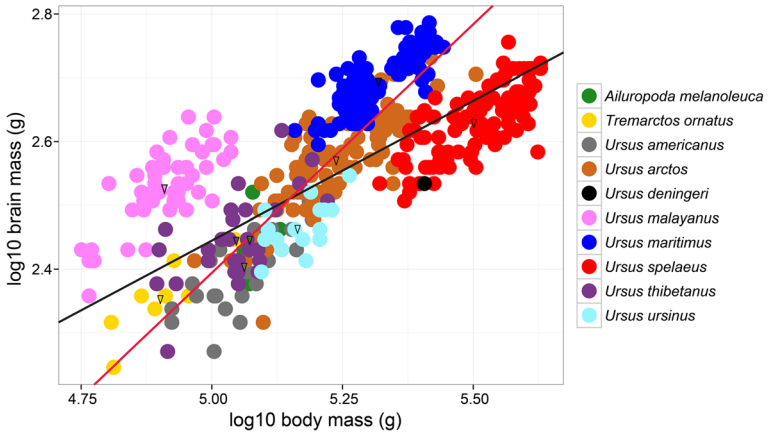

Fig. 1 Scatterplot of log10 brain mass (g) against log10 body mass (g) with a PGLS regression lines (phylogenetic generalized least squares). In black is the PGLS regression line for all data points (*p* value: 0.0148, slope: 0.43978, intercept: 0.24623, adjusted R^2: 0.5378), in red the PGLS regression line without *Ursus malayanus* and *Ursus spelaeus* (*p* value: 0.0016, slope: 0.78069, intercept: −1.50995, adjusted R^2: 0.8606). The triangles represent the mean for each species on which PGLS was calculated

residuals to test for significant differences. This was performed in R, version 3.2.3 [75], using the packages pgirmess and PMCMR [87, 88]. The subset of different brain volume estimations was analysed using a Wilcoxon signed-rank test for paired samples in R, version 3.2.3. [75]. Boxplots were created in the package ggplot2 [89].

I used squared-change parsimony [90] to reconstruct ancestral stages for log 10 average body mass (g), log 10 average brain mass (g), and averaged residuals respectively. This analysis follows a Brownian motion model of evolution [91]. The resulting ancestral character states were then used to investigate the relative mass change (in percent) from one node to the following within the tree. These analyses were performed for each variable separately in Mesquite software (version 3.01) [92].

To test for a possible effect of dormancy and diet on relative and absolute brain size, I scored each of these variables between 1 and 3: 1 represents states where a smaller brain size is expected and 3 the opposite. Dormancy was scored as 1 (dormancy), 2 (fasting periods), and 3 (no dormancy) [69]. Dietary preferences were scored using the compilation from van Heteren et al. [2]. The diet was scored between 1 (completely folivorous/low caloric diet) to 3 (completely faunivorous (high caloric diet) using the formula:

$$\begin{aligned}\text{Diet score} = {} & (\text{percent folivory/overall percent})^{*}1 \\ & +(\text{percent frugivory/overall percent})^{*}2 \\ & +(\text{percent faunivory/overall percent})^{*}3\end{aligned}$$

The scoring enables to multiply both scores to one under the assumption that unidirectional or opposing trends show a combined effect on brain size. This is possible because the array of possible variables is constrained among three states. I performed the Kendall's tau correlation analysis in R, version 3.2.3, using the package Kendall [93].

Results

The resulting averaged reconstructed body mass (g) and brain mass (g) with standard deviation as well as the ecological scores are given in Table 1.

The slopes of the OLS regression lines of the different bear species were not significantly different from each other. Intercepts, however, were in many cases significantly different among species (Table 2, Additional file 4: Table S3). The intercept of cave bears was not significantly different from that of *U. americanus* and *U. ursinus*.

U. spelaeus and *U. deningeri* have the lowest average residuals within the dataset, followed by *U. ursinus* and *U. americanus* (Fig. 2, Table 1). The highest average residuals were found in *U. malayanus* and *U. maritimus*. The Kruskal-Wallis test followed by a Dunn's test with Bonferroni adjustment revealed that the residuals of *U. spelaeus* are significantly smaller than of most other bear species, except for *U. ursinus* and *A. melanoleuca* (Table 3).

The biggest documented cave bear brain volume is 1.8 times bigger than the smallest. In comparison, in *U. arctos* it is 2.6 times bigger and in *U. thibetanus* 2.2 times. Polar bears, however, exhibit low variation with the biggest brain volume being 1.6 times bigger than the smallest (Table 1).

The comparison between different methods to estimate brain volumes revealed that external measurements produced results significantly different from brain volume measured directly with glass beads (Fig. 3). In *U. spelaeus*, brain volumes inferred by external measurements were significantly higher than those measured with soda lime glass beads (n = 15, median glass beads = 410 ml, median external measurements = 480 ml, V = 120, p-value = <0.0001). The opposite is true for *U. arctos* and *U. malayanus*. Here, brain volumes were significantly higher when measured with glass beads (*U. arctos*: n = 34, median glass beads = 370 ml, median external measurements = 312 ml, V = 66, p-value = <0.0001; *U. malayanus*: n = 9, median glass beads = 310 ml, median external measurements = 191 ml, V = 0, p-value = 0.0039).

The ancestral stage reconstruction based on squared-change parsimony revealed that the small relative brain size of *U. spelaeus* and *U. ursinus* represent a secondarily derived condition, as their respective ancestral stages exhibit a higher relative brain size (Fig. 2, Additional file 5: Table S4). The comparison between the relative change of body mass (g) and brain mass (g) shows that the evolution of a bigger body size in *U. spelaeus* outpaced brain size evolution. Both increased size compared to their ancestral stages, respectively; however, body size increased at a much higher pace. The reverse was found in *U. maritimus*, in which brain size evolution outpaced body size increase. Nonetheless, in *U. maritimus* and *U. spelaeus* brain as well as body size evolution are unidirectional towards increasing. In *U. americanus* the trend is unidirectional towards decrease. These cases contrast with the decoupling trend recorded for *U. malayanus*. In this species, the body size decreases where the brain size increases leading to the high relative brain size found in this species. At the basis of the tree, the analysis retrieved an ancestral body mass of 112,052 g and a brain mass of 277 g.

Using Kendall's tau to find correlations between ecological scores and brain mass (g) revealed no significant results. Residuals were not significantly correlated with dormancy or diet scores. However, residuals were correlated with the combined score (Table 4).

Discussion

Encephalization in Ursidae

U. spelaeus had a significantly smaller relative brain size than most extant bear species. The brain size variation in cave bears over time, between males and females [1] as well as high altitude and lowland populations [81] did not exceed the intraspecific variation in extant *U. americanus*,

Table 2 Results of the pairwise comparisons of slopes and intercepts among different bear species

	Ailuropoda melanoleuca	*Tremarctos ornatus*	*Ursus americanus*	*Ursus arctos*	*Ursus malayanus*	*Ursus maritimus*	*Ursus spelaeus*	*Ursus thibetanus*	*Ursus ursinus*
Ailuropoda melanoleuca		+/− 0.0034	+/− 0.0366	+/− 0.0306	+/− 0.1725*****	+/− 0.1086*****	+/− 0.0596***	+/− 0.0129	+/− 0.0347
Tremarctos ornatus	+/− 0.4053		+/− 0.0400**	+/− 0.0273	+/− 0.1691*****	+/− 0.1052*****	+/− 0.0630***	+/− 0.0096	+/− 0.0380*
Ursus americanus	+/− 0.3957	+/− 0.0096		+/− 0.0672*****	+/− 0.2091*****	+/− 0.1452*****	+/− 0.0230	+/− 0.0495*****	+/− 0.0019
Ursus arctos	+/− 0.3362	+/− 0.0691	+/− 0.0595		+/− 0.1419*****	+/− 0.0779*****	+/− 0.0903*****	+/− 0.0177	+/− 0.0653*****
Ursus malayanus	+/− 0.3895	+/− 0.0158	+/− 0.0062	+/− 0.0533		+/− 0.0639*****	+/− 0.2321*****	+/− 0.1596*****	+/− 0.2072*****
Ursus maritimus	+/− 0.2864	+/− 0.1189	+/− 0.1093	+/− 0.0498	+/− 0.1031		+/− 0.1682*****	+/− 0.0956*****	+/− 0.1432*****
Ursus spelaeus	+/− 0.2161	+/− 0.1892	+/− 0.1796	+/− 0.1200	+/− 0.1734	+/− 0.0702		+/− 0.0726*****	+/− 0.0250
Ursus thibetanus	+/− 0.2497	+/− 0.1556	+/− 0.1460	+/− 0.0865	+/− 0.1398	+/− 0.0367	+/− 0.0335		+/− 0.0476*****
Ursus ursinus	+/− 0.1606	+/− 0.2447	+/− 0.2351	+/− 0.1756	+/− 0.2289	+/− 0.1258	+/− 0.0555	+/− 0.0891	

Significant results are marked with stars (*p*-value: *< 0.5, **< 0.1, ***< 0.01, ****< 0.001, *****< 0.0001)
Upper triangle shows intercept comparisons and lower triangle shows slope comparisons

U. arctos, *U. malayanus*, and *U. thibetanus*. Especially, the relative brain size of *U. arctos* and *U. thibetanus* exhibits a considerable amount of variation. The study of brain size evolution often focuses on the evolution of increased encephalization and intelligence [38, 94–99]. Animals with bigger relative brain size often show more flexibility in behaviour and are potentially more adaptable [100–104]. Nonetheless, brain tissue is expensive and producing it comes at the cost of a slower life history [43–45, 57, 64, 105]. Therefore, in some species a secondary reduction of relative or absolute brain size was described [106]. Especially, islands represent a challenging habitat for many mammals and several species exhibit a secondary decrease in encephalization [107, 108]. Dormancy and diet, separately, were not correlated with brain size; however, the combination of both variables showed a significant effect. A possible explanation for this correlation could be that cave bears underwent a change in diet in a habitat in which they were still forced to rest during winters [1, 9] limiting the possibility of so called cognitive buffering [66, 109]. Under the Cognitive Buffer hypothesis, it is expected that relative brain size of mammals in highly seasonal environment increases due to the necessity of behavioural flexibility. This, however, also implies an active reaction towards the environmental change. In contrast, dormancy does not require this high level of behavioural flexibility but relies on body fat storage, which additionally has a negative trade-off with brain size [60, 66]. This suggests that brain size in cave bears might exhibit a physiological buffering effect [66] partly constraining relative brain size. Other bear species such as *U. arctos* and *U. americanus* would also exhibit this physiological buffering effect but their food quality or life history might lessen the constraint on relative brain size.

In Ursidae, three life history variables have been demonstrated to correlate with encephalization: gestation time (negative), newborn mass (positive), and litter size (negative) [57]. In *A. melanoleuca*, a combination of these variable with a year-round active strategy [69] is potentially the reason why the second herbivorous species in the dataset exhibits an encephalization higher than found in cave bears. Nonetheless, the life history correlates with encephalization are not unidirectional in the giant panda. In contrast, the highest encephalized species, *U. malayanus*, shows unidirectional trends towards increased encephalization in most variables with heavy newborns, small litter size, non-resting strategy, and 68% faunivory [2, 69, 110]. Gestation time and litter size are not known for *U. spelaeus*. However, cave bears were about the same size as *U. arctos* at birth [14, 111], contributing to its small relative brain size. A small relative brain size can already be traced in *U. deningeri*. This ancestor of *U. spelaeus* also exhibits low encephalization and is usually considered a herbivorous species with winter resting behaviour as well [25, 112].

The effect of diet alone on brain size in Ursidae remains elusive. In other groups such as primates and bats the link is more apparent. Fruit, blood, and meat eating bats tend to be more encephalized than their insect-eating relatives and in primates leaf-eaters are the least encephalized [67, 68]. Although a comparable link was proposed for Carnivora, it is hypothesized to be more

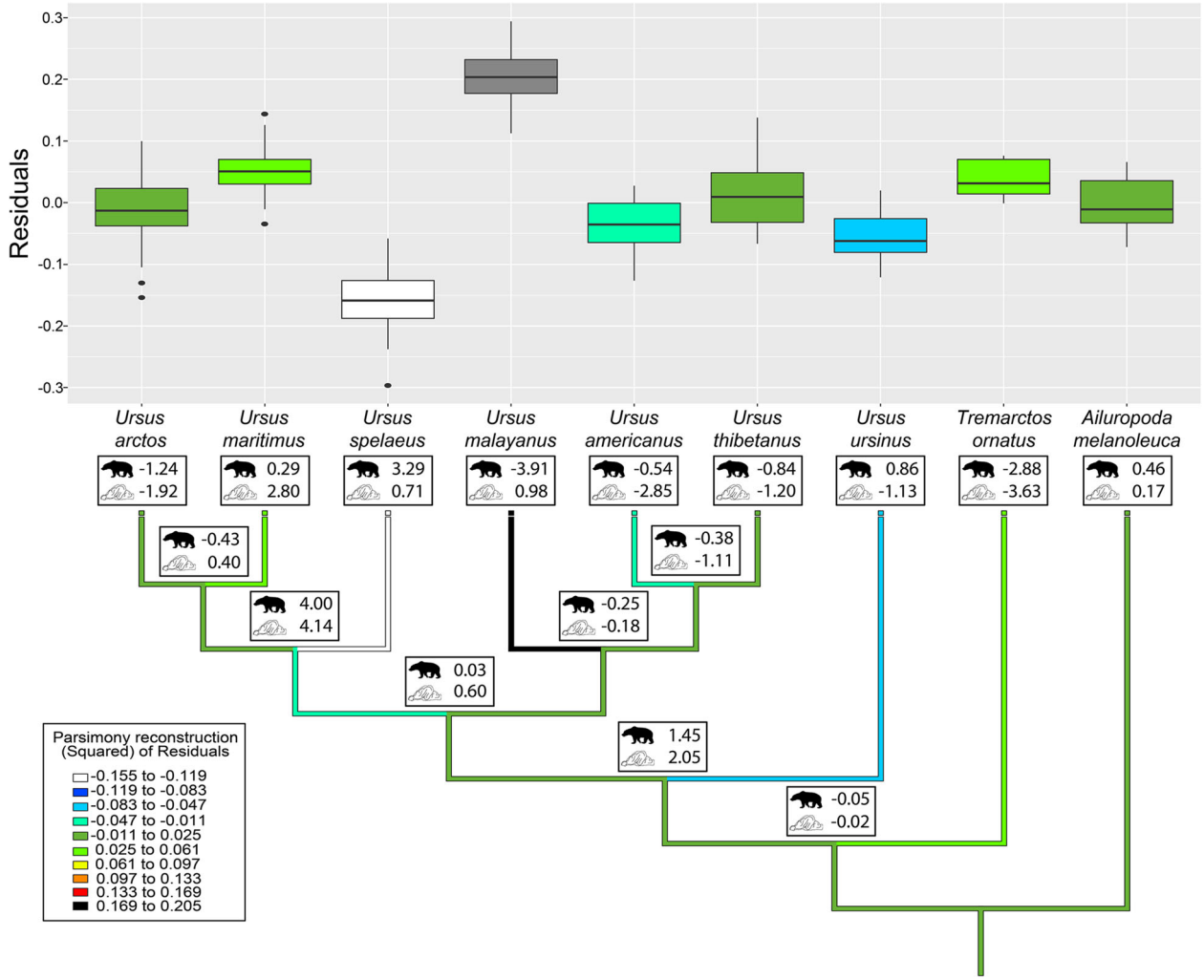

Fig. 2 Boxplots of the distribution of the residuals from PGLS (excluding *Ursus malayanus* and *Ursus spelaeus*) for Ursidae as well as result of the squared change parsimony analysis. Additionally, the relative change (in percent) of log10 body mass (g) and log10 brain mass (g) is shown in the boxes for every node. Terminal root value for log10 body size is 5.05 (112,052 g) and for log10 brain size 2.44 (277 g)

Table 3 Results of the Kruskal-Wallis rank sum test on the residuals of investigated bear species

Kruskal-Wallis rank sum test								
K-W chi-squared: 338.89 df: 8, *p*-value: <0.0001	*Ailuropoda melanoleuca*	*Tremarctos ornatus*	*Ursus americanus*	*Ursus arctos*	*Ursus malayanus*	*Ursus maritimus*	*Ursus thibetanus*	*Ursus ursinus*
Tremarctos ornatus	1.0000	-	-	-	-	-	-	-
Ursus americanus	1.0000	0.7560	-	-	-	-	-	-
Ursus arctos	1.0000	1.0000	1.0000	-	-	-	-	-
Ursus malayanus	0.0699	0.4557	**<0.0001**	**<0.0001**	-	-	-	-
Ursus maritimus	1.0000	1.0000	**<0.0001**	**<0.0001**	**0.0006**	-	-	-
Ursus thibetanus	1.0000	1.0000	0.8645	1.0000	**<0.0001**	0.7134	-	-
Ursus ursinus	1.0000	0.2586	1.0000	1.0000	**<0.0001**	**<0.0001**	0.2484	-
Ursus spelaeus	0.1133	**<0.0001**	**0.0005**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	0.2602

In bold are significant results

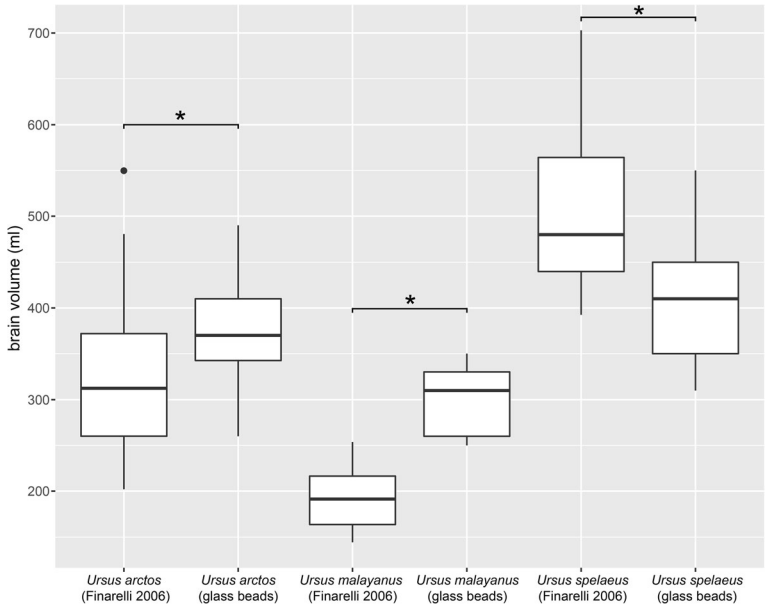

Fig. 3 Comparison between two methods for estimating brain volumes of Ursidae (asterisks mark significant differences based on a Wilcoxon signed-rank test)

associated with the process of acquiring food rather than the energetics of the diet itself [54, 67]. The change in diet in cave bears and associated smaller relative brain size is reminiscent of the often mentioned evolutionary arms-race between Carnivora and Ungulates in which Carnivora had to be more encephalized to outsmart their (herbivorous) prey [98]. This scenario, however, was later found to be unsubstantiated [113].

Smaers et al. [42] suggested that absolute brain size in the evolution of *U. spelaeus* was outpacing body size. This pattern was based on brain size estimates obtained by external measurements [37, 38, 74]. Although external measurements can predict brain volume with a certain confidence [74, 114], they can also have considerable prediction error [114]. The results of this study show that external measurements overestimate the endocranial volume of *U. spelaeus* (Fig. 3). The reason for this might be the frontal bossing found in cave bears likely caused by an extension of the frontal sinuses [16, 17, 35, 36, 41]. My results show that in cave bears body size evolution outpaced brain size evolution. Thus attesting to a remark by Marinelli [36]. Smaers et al. [42] also published brain and body size variables for three other extinct bear species *Arctodus simus* (3 Ma – 0.01 Ma), *Cephalogale ursinus* (23.8 Ma – 22.8 Ma), and *Indarctos oregonensis* (10.3 Ma – 5.3 Ma). With these values *C. ursinus* would be placed high above the regression line (residual: 0.33), *A. simus* close to the line (residual: 0.04), and *I. oregonensis* below the line (residual: –0.16). Fossil evidence has shown to change the results of suggested bidirectional evolution in brain size [99, 106]. However, in ursids, the cave bear lineage represents one of the least encephalized compared to extant and most extinct relatives.

On the methodology of body mass reconstruction

I calculated the mass of every specimen individually based on skull length [72]. My body mass estimates, generally, were well within the range of known body mass distribution for each species (Table 1) [69]. However, the estimations for polar bears, *U. maritimus*, are generally small. Thus, this animal might be closer to the range of other bear species such as *U. arctos* in the scatterplot (Fig. 1). It is, nonetheless, possible that the measured skulls are from individuals from the lower range of mass distribution of this species. The opposite is true for the two smaller bear species *U. malayanus* and *U. ursinus*. *U. malayanus* potentially could have even bigger brains compared to body size than in the presented dataset. *U. ursinus* would

Table 4 Results of Kendall's tau on different scores as well as the combination of both

	Diet score (d)		Dormancy score (d)		d*d	
	tau	*p*-value	tau	*p*-value	tau	*p*-value
Average brain mass (g)	0.1970	0.5294	–0.1360	0.7285	0.0000	1.0000
Residuals	0.3660	0.2084	0.3400	0.2976	**0.5560**	**0.0476**

In bold are significant correlations

be within the range of other extant bear species in the scatterplot (Fig. 1) such as *U. arctos*. *U. spelaeus* is considered to be one of the biggest carnivorans [115], with some estimates suggesting it to have surpassed the size of the polar bear or the Kodiak brown bear, *U. a. middendorffi*, by reaching a body mass of about 1′500 kg [1]. Based on this, the cave bear could have had an exceptionally small relative brain size. Considering the possible bias body mass estimations based on skull length had on the dataset, encephalization in Ursidae could be more even with two strong outliers, *U. malayanus* towards increased encephalization and *U. spelaeus* towards decreased one.

Conclusion

The aim of this study was to examine the encephalization in cave bears and comparing it with living and extinct members of Ursidae. *U. spelaeus*, and subsequently all potential species associated with this taxon, exhibit one of the lowest encephalization in Ursidae because body size increase outpaced brain size increase in its evolution. This is a trend observable early on in the cave bear lineage as is evidenced by the low encephalization of *U. deningeri*. My results stand in contrast to previous interpretations of cave bear brain evolution [42]. I showed that this study has used overestimated brain volumes due to the shape of cave bear skulls. Bear species, which do not exhibit dormancy and have a high caloric diet, showed a weak but significant correlation with bigger relative brain size. This would be in accordance with the trait-off between brain size and adipose tissue as well as studies on diet and brain size [60, 66–68]. The ecological shift towards a plant based diet alone did not affect encephalization in cave bears. However, a more general link associated with food acquirement strategy might still exist [67]. The herbivorous *U. spelaeus* has a small relative brain size possibly due to the combined effect of unequal body/brain size evolution and a seasonal environment in which dormancy was necessary for survival.

Additional files

Additional file 1:Table S1. Basicranial length, body mass estimates, brain volumes and brain mass for all examined bear skulls. (XLSX 33 kb)

Additional file 2: Table S2. Data subset of brain volume estimates based on external measurements by Finarelli [74] and glass bead method. (XLSX 12 kb)

Additional file 3: Supplementary Information. Results for different linear models and corresponding graphical output as well as boxplot on residuals based on PGLS with all species. (PDF 658 kb)

Additional file 4: Table S3. Additional results for slope and intercept pairwise comparisons. (XLSX 31 kb)

Additional file 5: Table S4. Node values for ancestral stage reconstructions. (XLSX 13 kb)

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Availability of data and materials

All data generated and/or analysed during this study are included in this published article and its supplementary information files.

Competing interests

I declare no competing interests of any kind.

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References

1. Rabeder G, Nagel D, Pacher M. Der Höhlenbär. Stuttgart: Thorbecke Verlag; 2000.
2. van Heteren AH, MacLarnon A, Soligo C, Rae TC. Functional morphology of the cave bear (*Ursus spelaeus*) mandible: a 3D geometric morphometric analysis. Org Divers Evol. 2016;16(1):299–314.
3. Knapp M, Rohland N, Weinstock J, Baryshnikov G, Sher A, Nagel D, et al. First DNA sequences from Asian cave bear fossils reveal deep divergences and complex phylogeographic patterns. Mol Ecol. 2009;18(6):1225–38.
4. Stuart AJ. Insularity and quaternary vertebrate faunas in Britain and Ireland. Geol Soc Spec Publ. 1995;96(1):111–25.
5. Garcia N, Arsuaga JL, Torres T. The carnivore remains from the Sima de los Huesos Middle Pleistocene site (sierra de Atapuerca, Spain). J Hum Evol. 1997;33(2):155–74.
6. Barnosky AD, Koch PL, Feranec RS, Wing SL, Shabel AB. Assessing the causes of Late Pleistocene extinctions on the continents. Science. 2004;306(5693):70–5.
7. Stuart AJ. Late quaternary megafaunal extinctions on the continents: a short review. Geol J. 2015;50(3):338–63.
8. Stiller M, Baryshnikov G, Bocherens H, Grandal d'Anglade A, Hilpert B, Münzel SC, et al. Withering away – 25,000 years of genetic decline preceded cave bear extinction. Mol Biol Evol 2010;27(5):975-978.
9. Pacher M, Stuart AJ. Extinction chronology and palaeobiology of the cave bear (*Ursus spelaeus*). Boreas. 2009;38(2):189–206.
10. Baca M, Popović D, Stefaniak K, Marciszak A, Urbanowski M, Nadachowski A, et al. Retreat and extinction of the Late Pleistocene cave bear *(Ursus spelaeus* Sensu Lato). Sci Nat. 2016;103(11):92.
11. Krause J, Unger T, Noçon A, Malaspinas A-S, Kolokotronis S-O, Stiller M, et al. Mitochondrial genomes reveal an explosive radiation of extinct and extant bears near the Miocene-Pliocene boundary. BMC Evol Biol. 2008;8(1):1–12.
12. Bon C, Caudy N, de Dieuleveult M, Fosse P, Philippe M, Maksud F, et al. Deciphering the complete mitochondrial genome and phylogeny of the extinct cave bear in the Paleolithic painted cave of Chauvet. PNAS. 2008; 105(45):17447–52.
13. Loreille O, Orlando L, Patou-Mathis M, Philippe M, Taberlet P, Hanni C. Ancient DNA analysis reveals divergence of the cave bear, *Ursus spelaeus*, and brown bear, *Ursus arctos*, lineages. Curr Biol. 2001;11(3):200–3.
14. Ehrenberg K. Die Variabilität der Backenzähne beim Höhlenbären. In: Abel O, Kyrle G, editors. Die Drachenhöhle bei Mixnitz. Speläologische Monographien 7/8. Wien: Österreichische Staatsdruckerei; 1931. p. 537-573.

15. Abel O. Das Lebensbild der eiszeitlichen Tierwelt der Drachenhöhle bei Mixnitz. In: Abel O, Kyrle G, editors. Die Drachenhöhle bei Mixnitz. Speläologische Monographien 7/8. Wien: Österreichische Staatsdruckerei; 1931. p. 885-920.
16. Kurtén B. The cave bear story. New York: Columbia University Press; 1976.
17. Kurtén B. Pleistocene mammals of Europe. Chicago: Aldine; 1968.
18. Thenius E. Zähne und Gebiß der Säugetiere. Berlin: W. de Gruyter; 1989.
19. van Heteren AH, MacLarnon A, Soligo C, Rae TC. Functional morphology of the cave bear (*Ursus spelaeus*) cranium: a three-dimensional geometric morphometric analysis. Quat Int. 2014;339:209–16.
20. Naito YI, Germonpré M, Chikaraishi Y, Ohkouchi N, Drucker DG, Hobson KA, et al. Evidence for herbivorous cave bears (*Ursus spelaeus*) in Goyet cave, Belgium: implications for palaeodietary reconstruction of fossil bears using amino acid δ15N approaches. J Quat Sci. 2016;31(6):598–606.
21. Münzel SC, Rivals F, Pacher M, Döppes D, Rabeder G, Conard NJ, et al. Behavioural ecology of Late Pleistocene bears (*Ursus spelaeus*, *Ursus ingressus*): Insight from stable isotopes (C, N, O) and tooth microwear. Quat Int. 2014;339–340:148–63.
22. Bocherens H, Stiller M, Hobson KA, Pacher M, Rabeder G, Burns JA, et al. Niche partitioning between two sympatric genetically distinct cave bears (*Ursus spelaeus* and *Ursus ingressus*) and brown bear (*Ursus arctos*) from Austria: isotopic evidence from fossil bones. Quat Int. 2011;245(2):238–48.
23. Bocherens H, Drucker DG, Billiou D, Geneste J-M, van der Plicht J. Bears and humans in Chauvet cave (Vallon-Pont-d'Arc, Ardèche, France): insights from stable isotopes and radiocarbon dating of bone collagen. J Hum Evol. 2006;50(3):370–6.
24. Bocherens H, Billiou D, Patou-Mathis M, Bonjean D, Otte M, Mariotti A. Paleobiological implications of the isotopic signatures (13C,15N) of fossil mammal collagen in Scladina cave (Sclayn, Belgium). Quat Res. 1997;48(3):370–80.
25. Bocherens H, Fizet M, Mariotti A. Diet, physiology and ecology of fossil mammals as inferred from stable carbon and nitrogen isotope biogeochemistry: implications for Pleistocene bears. Palaeogeogr Palaeoclimatol Palaeoecol. 1994;107(3):213–25.
26. Richards MP, Pacher M, Stiller M, Quilès J, Hofreiter M, Constantin S, et al. Isotopic evidence for omnivory among European cave bears: Late Pleistocene *Ursus spelaeus* from the Peştera cu Oase, Romania. PNAS. 2008;105(2):600–4.
27. Robu M, Fortin JK, Richards MP, Schwartz CC, Wynn JG, Robbins CT, et al. Isotopic evidence for dietary flexibility among European Late Pleistocene cave bears (*Ursus spelaeus*). Can J Zool. 2013;91(4):227–34.
28. Meloro C. Feeding habits of Plio-Pleistocene large carnivores as revealed by the mandibular geometry. J Vert Paleontol. 2011;31(2):428–46.
29. Figueirido B, Palmqvist P, Pérez-Claros JA. Ecomorphological correlates of craniodental variation in bears and paleobiological implications for extinct taxa: an approach based on geometric morphometrics. J Zool. 2009;277(1):70–80.
30. Jones BD, DeSantis LRG. Dietary ecology of the extinct cave bear: evidence of omnivory as inferred from dental microwear textures. Acta Palaeontol Pol. 2016;61(4):735–41.
31. Peigné S, Goillot C, Germonpré M, Blondel C, Bignon O, Merceron G. Predormancy omnivory in European cave bears evidenced by a dental microwear analysis of *Ursus spelaeus* from Goyet, Belgium. PNAS. 2009; 106(36):15390–3.
32. Rabal-Garcés R, Cuenca-Bescós G, Ignacio Canudo J, De Torres T. Was the European cave bear an occasional scavenger? Lethaia. 2012;45(1):96–108.
33. Bocherens H. Isotopic tracking of large carnivore palaeoecology in the mammoth steppe. Quat Sci Rev. 2015;117:42–71.
34. Edinger T. Über einige fossile Gehirne. Paläont Z. 1928;9(4):379–402.
35. Über DH. Hirnschädelausgüsse von *Ursus spelaeus*. In: Abel O, Kyrle G, editors. Die Drachenhöhle bei Mixnitz. Speläologische Monographien 7/8. Wien: Österreichische Staatsdruckerei; 1931. p. 498–536.
36. Marinelli W. Bericht über die Untersuchung der Höhlenbärenschädel. In: Abel O, Kyrle G, editors. Die Drachenhöhle bei Mixnitz. Speläologische Monographien 7/8. Wien: Österreichische Staatsdruckerei; 1931. p. 332–497.
37. Finarelli JA, Flynn JJ. Brain-size evolution and sociality in Carnivora. PNAS. 2009;106(23):9345–9.
38. Finarelli JA, Flynn JJ. The evolution of encephalization in caniform carnivorans. Evolution. 2007;61(7):1758–72.
39. Groiss JT. Untersuchungen der Gehirnmorphologie von *Ursus deningeri* v. REICHENAU und von *Ursus spelaeus* ROSENMÜLLER (Mammalia, Ursidae) an Schädelausgüssen quartärer Funde aus österreichischen Höhlen. Abh Geol B-A. 1994;50:115–23.
40. Santos E, Garcia N, Carretero JM, Arsuaga JL, Tsoukala E. Endocranial traits of the Sima de los Huesos (Atapuerca, Spain) and Petralona (Chalkidiki, Greece) Middle Pleistocene ursids. Phylogenetic and biochronological implications. Ann Paleontol. 2014;100(4):297–309.
41. García N, Santos E, Arsuaga JL, Carretero JM. Endocranial morphology of the *Ursus deningeri* von Reichenau 1904 from the Sima de los Huesos (sierra de Atapuerca) Middle Pleistocene site. J Vert Paleontol. 2007;27(4):1007–17.
42. Smaers JB, Dechmann DKN, Goswami A, Soligo C, Safi K. Comparative analyses of evolutionary rates reveal different pathways to encephalization in bats, carnivorans, and primates. PNAS. 2012;109(44):18006–11.
43. Isler K, van Schaik CP. The expensive brain: a framework for explaining evolutionary changes in brain size. J Hum Evol. 2009;57(4):392–400.
44. Mink JW, Blumenschine RJ, Adams DB. Ratio of central nervous system to body metabolism in vertebrates: its constancy and functional basis. Am J Physiol Regul Integr Comp Physiol. 1981;241(3):R203–R12.
45. Aiello LC, Bates N, Joffe T. In defense of the expensive tissue hypothesis. In: Falk D, Gibson KR, editors. Evolutionary Anatomy of the primate Cerebral Cortex. Cambridge: Cambridge University Press; 2001. p. 57–78.
46. Dunbar RIM. The social brain hypothesis. Evol Anthropol. 1998;6(5):178–90.
47. Pérez-Barbería FJ, Shultz S, Dunbar RIM, Janis C. Evidence for coevolution of sociality and relative brain size in three orders of mammals. Evolution. 2007; 61(12):2811–21.
48. Shultz S, Dunbar RIM. Both social and ecological factors predict ungulate brain size. Proc Biol Sci. 2006;273(1583):207–15.
49. Taylor AB, van Schaik CP. Variation in brain size and ecology in *Pongo*. J Hum Evol. 2007;52(1):59–71.
50. van Woerden JT, van Schaik CP, Isler K. Effects of seasonality on brain size evolution: evidence from strepsirrhine primates. Am Nat. 2010; 176(6):758–67.
51. van Woerden JT, Willems EP, van Schaik CP, Isler K. Large brains buffer energetic effects of seasonal habitats in Catarrhine primates. Evolution. 2012;66(1):191–9.
52. Weisbecker V, Blomberg S, Goldizen AW, Brown M, Fisher D. The evolution of relative brain size in marsupials is energetically constrained but not driven by behavioral complexity. Brain Behav Evol. 2015;85(2):125–35.
53. Garamszegi LZ, Møller AP, Erritzøe J. Coevolving avian eye size and brain size in relation to prey capture and nocturnality. Proc Biol Sci. 2002; 269(1494):961–7.
54. Gittleman JL. Carnivore brain size, behavioral ecology, and phylogeny. J Mammal. 1986;67(1):23–36.
55. Mace GM, Harvey PH, Clutton-Brock TH. Brain size and ecology in small mammals. J Zool. 1981;193(3):333–54.
56. Eisenberg JF, Wilson DE. Relative brain size and feeding strategies in the Chiroptera. Evolution. 1978;32(4):740–51.
57. Finarelli JA. Does encephalization correlate with life history or metabolic rate in Carnivora? Biol Lett. 2010;6(3):350–3.
58. Raichlen DA, Gordon AD. Relationship between exercise capacity and brain size in mammals. PLoS One. 2011;6(6):e20601.
59. Eisenberg JF, Wilson DE. Relative brain size and demographic strategies in didelphid marsupials. Am Nat. 1981;118(1):1–15.
60. Navarrete A, van Schaik CP, Isler K. Energetics and the evolution of human brain size. Nature. 2011;480(7375):91–3.
61. Barton RA, Capellini I. Maternal investment, life histories, and the costs of brain growth in mammals. PNAS. 2011;108(15):6169–74.
62. Isler K, van Schaik CP. Metabolic costs of brain size evolution. Biol Lett. 2006; 2(4):557–60.
63. Weisbecker V, Goswami A. Brain size, life history, and metabolism at the marsupial/placental dichotomy. PNAS. 2010;107(37):16216–21.
64. Barrickman NL, Bastian ML, Isler K, van Schaik CP. Life history costs and benefits of encephalization: a comparative test using data from long-term studies of primates in the wild. J Hum Evol. 2008;54(5):568–90.
65. Western D. Size, life history and ecology in mammals. Afr J Ecol. 1979;17(4): 185–204.
66. Heldstab SA, van Schaik CP, Isler K. Being fat and smart: a comparative analysis of the fat-brain trade-off in mammals. J Hum Evol. 2016;100:25–34.
67. Striedter GF. Principles of brain evolution. Sunderland: Sinauer Associates; 2005.
68. DeCasien AR, Williams SA, Higham JP. Primate brain size is predicted by diet but not sociality. Nat Ecol Evol. 2017;1:0112.
69. Hunter L. Carnivores of the world. Princeton (New Jersey): Princeton University Press; 2011.
70. Lyman CP, Willis JS, Malan A, Wang LCH. Hibernation and torpor in mammals and birds. New York: Academic Press; 1982.
71. Logan CJ, Clutton-Brock TH. Validating methods for estimating endocranial volume in individual red deer (*Cervus elaphus*). Behav Process. 2013;92:143–6.

72. van Valkenburgh B. Skeletal and dental predictors of body mass in carnivores. In: Damuth J, Macfadden BJ, editors. Body size in mammalian paleobiology: estimation and biological implications. Cambridge: Cambridge University Press; 1990. p. 181–206.
73. Ebinger P. A cytarquitectonic volumetric comparison of brains in wild and domestic sheep. Z Anat Entwickl-Gesch. 1974;144:267–302.
74. Finarelli JA. Estimation of endocranial volume through the use of external skull measures in the Carnivora (Mammalia). J Mammal. 2006;87(5):1027–36.
75. R Development Core Team. R: A language and environment for statistical computing. Version 3.2.3. 2015. http://www.R-project.org. Accessed 10 Dec 2015.
76. Paradis E, Claude J, Strimmer K. APE: analyses of phylogenetics and evolution in R language. Bioinformatics. 2004;20:289–90.
77. Orme D, Freckleton R, Thomas G, Petzoldt T, Fritz S, Isaac N, et al. caper: comparative analyses of phylogenetics and evolution in R. R package version 0.5.2. 2013. https://CRAN.R-project.org/package=caper. Accessed 25 Jan 2016.
78. Kutschera VE, Bidon T, Hailer F, Rodi JL, Fain SR, Janke A. Bears in a forest of gene trees: Phylogenetic inference is complicated by incomplete lineage sorting and gene flow. Mol Biol Evol. 2014;31(8):2004–17.
79. Noonan JP, Hofreiter M, Smith D, Priest JR, Rohland N, Rabeder G. Genomic sequencing of Pleistocene cave bears. Science. 2005;309(5734):597–9.
80. Rabeder G, Hofreiter M. Der neue Stammbaum der alpinen Höhlenbären. Die Höhle. 2004;55:58–77.
81. Rabeder G, Hofreiter M, Nagel D, Withalm G. New taxa of Alpine cave bears (Ursidae, Carnivora). Cah Sci. 2004;2:49–67.
82. Rabeder G, Debeljak I, Hofreiter M, Withalm G. Morphological responses of cave bears (*Ursus spelaeus* group) to high-alpine habitats. Die Höhle. 2008; 59:59–72.
83. Dabney J, Knapp M, Glocke I, Gansauge M-T, Weihmann A, Nickel B, et al. Complete mitochondrial genome sequence of a Middle Pleistocene cave bear reconstructed from ultrashort DNA fragments. PNAS. 2013;110(39): 15758–63.
84. Baca M, Mackiewicz P, Stankovic A, Popović D, Stefaniak K, Czarnogórska K, et al. Ancient DNA and dating of cave bear remains from Niedźwiedzia Cave suggest early appearance of *Ursus ingressus* in Sudetes. Quat Int. 2014; 339–340:217–23.
85. Stiller M, Molak M, Prost S, Rabeder G, Baryshnikov G, Rosendahl W, et al. Mitochondrial DNA diversity and evolution of the Pleistocene cave bear complex. Quat Int. 2014;339–340:224–31.
86. Nyakatura K, Bininda-Emonds OR. Updating the evolutionary history of Carnivora (Mammalia): a new species-level supertree complete with divergence time estimates. BMC Biol. 2012;10(1):1–31.
87. Giraudoux P. pgirmess: data analysis in ecology. R package version 1.6.3. 2015. https://CRAN.R-project.org/package=pgirmess. Accessed 22 Jan 2016.
88. Pohlert G. The pairwise multiple comparison of mean ranks package (PMCMR). 2014. http://CRAN.R-project.org/package=PMCMR. Accessed 22 Jan 2016.
89. Wickham H. ggplot2: elegant graphics for data analysis. New York: Springer-Verlag; 2009.
90. Maddison WP. Squared-change parsimony reconstructions of ancestral states for continuous-valued characters on a phylogenetic tree. Syst Zool. 1991;40(3):304–14.
91. Germain D, Laurin M. Evolution of ossification sequences in salamanders and urodele origins assessed through event-pairing and new methods. Evol Dev. 2009;11(2):170–90.
92. Maddison WP, Maddison DR. Mesquite: a modular system for evolutionary analysis. Version 2.75. 2011. http://mesquiteproject.org. Accessed 10 Dec 2014.
93. McLeod AI. Kendall: Kendall rank correlation and Mann-Kendall trend test. R package version 2.2. 2011. https://CRAN.R-project.org/package=Kendall. Accessed 9 May 2016.
94. Kaskan PM, Finlay BL. Encephalization and its developmental structure: how many ways can a brain get big? In: Falk D, Gibson KR, editors. Evolutionary Anatomy of the primate Cerebral Cortex. Cambridge: Cambridge University Press; 2001. p. 14–29.
95. Gibson KR, Rumbaugh D, Beran M. Bigger is better: primate brain size in relationship to cognition. In: Falk D, Gibson KR, editors. Evolutionary Anatomy of the primate Cerebral Cortex. Cambridge: Cambridge University Press; 2001. p. 79–97.
96. Hofman MA. Evolution of the human brain: when bigger is better. Front Neuroanat. 2014;8:15.
97. Roth G, Dicke U. Evolution of the brain and intelligence. Trends Cogn Sci. 2005;9(5):250–7.
98. Jerison HJ. Evolution of the brain and intelligence. New York: Academic Press; 1973.
99. Yao L, Brown JP, Stampanoni M, Marone F, Isler K, Martin RD. Evolutionary change in the brain size of bats. Brain Behav Evol. 2012;80(1):15–25.
100. Edmunds NB, Laberge F, McCann KS. A role for brain size and cognition in food webs. Ecol Lett. 2016;19(8):948–55.
101. Lefebvre L, Whittle P, Lascaris E, Finkelstein A. Feeding innovations and forebrain size in birds. Anim Behav. 1997;53(3):549–60.
102. Ratcliffe JM, Fenton MB, Shettleworth SJ. Behavioral flexibility positively correlated with relative brain volume in predatory bats. Brain Behav Evol. 2006;67(3):165–76.
103. Reader SM, Laland KN. Social intelligence, innovation, and enhanced brain size in primates. PNAS. 2002;99(7):4436–41.
104. Lefebvre L, Reader SM, Sol D. Brains, innovations and evolution in birds and primates. Brain Behav Evol. 2004;63(4):233–46.
105. Weisbecker V, Goswami A. Reassessing the relationship between brain size, life history, and metabolism at the marsupial/placental dichotomy. Zool Sci. 2014;31(9):608–12.
106. Safi K, Seid MA, Dechmann DKN. Bigger is not always better: when brains get smaller. Biol Lett. 2005;1(3):283–6.
107. Köhler M, Moyà-Solà S. Reduction of brain and sense organs in the fossil insular bovid *Myotragus*. Brain Behav Evol. 2004;63(3):125–40.
108. Weston EM, Lister AM. Insular dwarfism in hippos and a model for brain size reduction in *Homo floresiensis*. Nature. 2009;459(7243):85–8.
109. Sol D. Revisiting the cognitive buffer hypothesis for the evolution of large brains. Biol Lett. 2009;5(1):130–3.
110. Tacutu R, Craig T, Budovsky A, Wuttke D, Lehmann G, Taranukha D, et al. Human ageing genomic resources: integrated databases and tools for the biology and genetics of ageing. Nucleic Acids Res. 2013;41(D1):D1027–D33.
111. Ehrenberg K. Ein fast vollständiges Höhlenbärenneonatenskelett aus der Salzofenhöhle im Toten Gebirge. Ann Nathist Mus Wien. 1973;77:69–113.
112. Stiner MC. Mortality analysis of Pleistocene bears and its paleoanthropological relevance. J Hum Evol. 1998;34(3):303–26.
113. Radinsky L. Evolution of brain size in carnivores and ungulates. Am Nat. 1978;112(987):815–31.
114. Soul LC, Benson RBJ, Weisbecker V. Multiple regression modeling for estimating endocranial volume in extinct Mammalia. Paleobiology. 2012; 39(1):149–62.
115. Christiansen P. What size were *Arctodus simus* and *Ursus spelaeus* (Carnivora: Ursidae)? Ann Zool Fenn. 1999;36(2):93–102.

Additional file 1:Table S1. Basicranial length, body mass estimates, brain volumes and brain mass for all examined bear skulls. (XLSX 33 kb)

Species	Number	SKL	Body Mass (g)	Brain Vol (ml)	Brain Mass (g)
Ailuropoda melanoleuca	MNHN 2000-363	276	135'094.09	280	290.08
Ailuropoda melanoleuca	MNHN A 1729	244	105'324.03	270	279.72
Ailuropoda melanoleuca	ZMB_Mam_17542	258	117'888.60	230	238.28
Ailuropoda melanoleuca	ZMB_Mam_85761	260	119'741.90	320	331.52
Ailuropoda melanoleuca	ZMB_Mam_17246	255	115'136.01	260	269.36
Tremarctos ornatus	ZMB_Mam_6121	226	90'219.22	220	227.92
Tremarctos ornatus	ZMB_Mam_34455	204	73'358.92	220	227.92
Tremarctos ornatus	ZMUZH 17571	191	64'222.53	200	207.2
Tremarctos ornatus	ZMUZH 17597	210	77'782.69	210	217.56
Tremarctos ornatus	NMBE 1042648	250	110'621.32	270	279.72
Tremarctos ornatus	ZMA 882 (NBC)	192	64'903.55	170	176.12
Tremarctos ornatus	MNHN 1990-696	215	81'569.10	220	227.92
Tremarctos ornatus	MNHN 1992-1469	219	84'663.67	250	259
Ursus americanus	ZMB_Mam_69392	228	91'839.26	230	238.28
Ursus americanus	ZMB_Mam_69390	237	99'309.70	250	259
Ursus americanus	ZMB_Mam_23162	263	122'549.24	260	269.36
Ursus americanus	ZMB_Mam_14388	258	117'888.60	270	279.72
Ursus americanus	ZMB_Mam_87102	239	101'009.86	180	186.48
Ursus americanus	ZMB_Mam_87106	218	83'884.58	200	207.2
Ursus americanus	ZMB_Mam_87104	286	145'164.15	260	269.36
Ursus americanus	ZMB_Mam_87103	295	154'539.84	340	352.24
Ursus americanus	ZMB_Mam_87101	269	128'262.47	250	259
Ursus americanus	ZMB_Mam_69404	252	112'416.25	250	259
Ursus americanus	NMBE 1021778	242	103'587.43	260	269.36
Ursus americanus	NMBE 1042659	296	155'599.88	290	300.44
Ursus americanus	ZMA no nmb (NBC)	257	116'967.42	240	248.64
Ursus americanus	ZMA 24412 (NBC)	264	123'492.32	300	310.8
Ursus americanus	RN 547 (NBC)	294	153'483.47	310	321.16
Ursus americanus	RN no nmb (NBC)	230	93'473.87	220	227.92
Ursus americanus	RN no nmb (NBC)	245	106'197.79	210	217.56
Ursus americanus	RN 16866 (NBC)	239	101'009.86	220	227.92
Ursus americanus	MNHN 2006-442	283	142'104.75	280	290.08
Ursus americanus	MNHN 1990-496	271	130'196.10	280	290.08
Ursus americanus	MNHN 1938-125	254	114'225.77	220	227.92
Ursus americanus	MNHN 1935-194	218	83'884.58	210	217.56
Ursus americanus	MNHN 1902-1415	252	112'416.25	230	238.28
Ursus americanus	MNHN Ca. E. 493	261	120'674.03	280	290.08
Ursus americanus	MNHN 2006-418	269	128'262.47	250	259
Ursus americanus	MNHN 1990-495	240	101'865.40	220	227.92
Ursus americanus	MNHN A 2137	253	113'319.19	200	207.2
Ursus americanus	MNHN A 2138	262	121'609.81	230	238.28
Ursus arctos	ZMB_Mam_11069	296	155'599.88	310	321.16
Ursus arctos	ZMB_Mam_5584	296	155'599.88	320	331.52
Ursus arctos	ZMB_Mam_10356	305	165'304.88	340	352.24
Ursus arctos	ZMB_Mam_3386	325	187'933.58	350	362.6
Ursus arctos	ZMB_Mam_14395	287	146'191.27	320	331.52
Ursus arctos	ZMB_Mam_13383	264	123'492.32	300	310.8

Ursus arctos	ZMB_Mam_14402	345	212’028.66	370	383.32
Ursus arctos	ZMB_Mam_12008	340	205’867.32	360	372.96
Ursus arctos	ZMB_Mam_13728	273	132’144.33	310	321.16
Ursus arctos	ZMB_Mam_11377	366	238’908.61	420	435.12
Ursus arctos	ZMB_Mam_14392	383	261’855.39	520	538.72
Ursus arctos	ZMB_Mam_11081	324	186’767.33	420	435.12
Ursus arctos	ZMB_Mam_14391	350	218’281.76	420	435.12
Ursus arctos	ZMB_Mam_13246	292	151’381.69	360	372.96
Ursus arctos	ZMB_Mam_14413	321	183’290.59	350	362.6
Ursus arctos	ZMB_Mam_14401	343	209’553.12	400	414.4
Ursus arctos	ZMB_Mam_14412	314	175’306.45	330	341.88
Ursus arctos	ZMB_Mam_29294	346	213’271.94	420	435.12
Ursus arctos	ZMB_Mam_28473	285	144’140.70	390	404.04
Ursus arctos	ZMB_Mam_22197	267	126’343.45	270	279.72
Ursus arctos	ZMB_Mam_28470	353	222’077.68	350	362.6
Ursus arctos	ZMB_Mam_15637	311	171’939.63	320	331.52
Ursus arctos	ZMB_Mam_45395	340	205’867.32	420	435.12
Ursus arctos	ZMB_Mam_35488	297	156’663.57	290	300.44
Ursus arctos	ZMB_Mam_37701	320	182’139.00	410	424.76
Ursus arctos	ZMB_Mam_45413	248	108’840.97	250	259
Ursus arctos	ZMB_Mam_48858	293	152’430.75	320	331.52
Ursus arctos	ZMB_Mam_87121	281	140’083.43	320	331.52
Ursus arctos	ZMB_Mam_87110	299	158’801.94	320	331.52
Ursus arctos	ZMB_Mam_69343	229	92’654.75	250	259
Ursus arctos	ZMB_Mam_69366	307	167’501.82	330	341.88
Ursus arctos	ZMB_Mam_69344	284	143’120.90	300	310.8
Ursus arctos	ZMB_Mam_52810	373	248’228.61	420	435.12
Ursus arctos	ZMB_Mam_69341	343	209’553.12	390	404.04
Ursus arctos	ZMB_Mam_51247	294	153’483.47	370	383.32
Ursus arctos	ZMB_Mam_69369	349	217’023.80	440	455.84
Ursus arctos	ZMB_Mam_69394	317	178’706.24	440	455.84
Ursus arctos	ZMB_Mam_69368	316	177’569.31	370	383.32
Ursus arctos	ZMB_Mam_69342	256	116’049.89	250	259
Ursus arctos	ZMB_Mam_87131	293	152’430.75	350	362.6
Ursus arctos	ZMB_Mam_93300	295	154’539.84	350	362.6
Ursus arctos	ZMB_Mam_87147	304	164’211.90	360	372.96
Ursus arctos	ZMUZH 10310	314	175’306.45	350	362.6
Ursus arctos	ZMUZH 10158	302	162’036.94	370	383.32
Ursus arctos	NMBE 1054621	358	228’477.65	400	414.4
Ursus arctos horribilis	NMBE 1054540	364	236’278.82	420	435.12
Ursus arctos	NMBE 1042563	268	127’301.14	260	269.36
Ursus arctos	NMBE 1042418	358	228’477.65	400	414.4
Ursus arctos	NMBE 1030173	356	225’906.64	430	445.48
Ursus arctos	NMBE 1042417	315	176’436.05	360	372.96
Ursus arctos	NMBE 1042343	352	220’808.70	420	435.12
Ursus arctos	NMBE 1042384	295	154’539.84	340	352.24
Ursus arctos	NMBE 1047854	302	162’036.94	320	331.52
Ursus arctos	NMBE 1042355	286	145’164.15	340	352.24
Ursus arctos	NMBE 1042396	295	154’539.84	390	404.04
Ursus arctos	NMBE 1042361	265	124’439.04	330	341.88
Ursus arctos	NMBE 1042364	319	180’991.08	420	435.12

Ursus arctos	NMBE 1042395	361	232’361.70	420	435.12
Ursus arctos	NMBE 1042363	274	133’123.93	340	352.24
Ursus arctos	NMBE 1042426	286	145’164.15	350	362.6
Ursus arctos	NMBE 1042366	292	151’381.69	410	424.76
Ursus arctos	NMBE 1042410	354	223’350.33	490	507.64
Ursus arctos	NMBE 1030241	338	203’428.47	460	476.56
Ursus arctos	NMBE 1042372	274	133’123.93	300	310.8
Ursus arctos	NMBE 1042376	327	190’277.07	390	404.04
Ursus arctos	NMBE 1042369	342	208’320.85	380	393.68
Ursus arctos	NMBE 1042379	355	224’626.65	410	424.76
Ursus arctos	NMBE 1042394	294	153’483.47	420	435.12
Ursus arctos	NMBE 1054620	283	142’104.75	380	393.68
Ursus arctos	NMBE 1042374	288	147’222.04	350	362.6
Ursus arctos	NMBE 1042390	276	135’094.09	310	321.16
Ursus arctos	NMBE 1042381	307	167’501.82	360	372.96
Ursus arctos syriacus	NMBE 1042413	326	189’103.49	370	383.32
Ursus arctos	NMBE 1042414	336	201’004.30	360	372.96
Ursus arctos	NMBE 1042383	307	167’501.82	370	383.32
Ursus arctos	NMBE 1042399	277	136’084.65	310	321.16
Ursus arctos	NMBE 1042393	309	169’713.40	410	424.76
Ursus arctos	NBC 2842/2	275	134’107.18	310	321.16
Ursus arctos	NBC no nmb	347	214’518.89	400	414.4
Ursus arctos	ZAM 9080 (NBC)	322	184’445.84	380	393.68
Ursus arctos syriacus	ZAM 22960 (NBC)	262	121’609.81	270	279.72
Ursus arctos syriacus	ZAM 16874 (NBC)	292	151’381.69	300	310.8
Ursus arctos	ZAM A883 (NBC)	266	125’389.42	200	207.2
Ursus arctos	ZAM 9081 (NBC)	284	143’120.90	320	331.52
Ursus arctos	RN 4876 (NBC)	289	148’256.47	320	331.52
Ursus arctos	ZMA 901 (NBC)	344	210’789.05	480	497.28
Ursus arctos	RN 2254 (NBC)	353	222’077.68	430	445.48
Ursus arctos horribilis	MNHN 2000-482	346	213’271.94	410	424.76
Ursus arctos horribilis	MNHN 1899-21	353	222’077.68	330	341.88
Ursus arctos horribilis	MNHN 2006-446	341	207’092.25	400	414.4
Ursus arctos middendorffi	NMBE 1042555	423	320’042.42	490	507.64
Ursus arctos middendorffi	NMBE 1042557	389	270’207.99	470	486.92
Ursus arctos middendorffi	NMBE 1042556	341	207’092.25	390	404.04
Ursus deningeri	Petralona PEC 1002 (AUTH)	378	254’996.04	330	341.88
Ursus malayanus	ZMB_Mam_8626	225	89’414.65	300	310.8
Ursus malayanus	ZMB_Mam_17531	221	86’232.78	330	341.88
Ursus malayanus	ZMB_Mam_85773	228	91’839.26	380	393.68
Ursus malayanus	ZMB_Mam_17533	214	80’804.55	350	362.6
Ursus malayanus	ZMB_Mam_85774	205	74’087.13	310	321.16
Ursus malayanus	ZMB_Mam_15638	198	69’065.90	260	269.36
Ursus malayanus	ZMB_Mam_17245	200	70’482.38	300	310.8
Ursus malayanus	ZMB_Mam_85770	221	86’232.78	310	321.16
Ursus malayanus	ZMB_Mam_14377	238	100’157.96	380	393.68
Ursus malayanus	ZMB_Mam_17532	211	78’532.71	370	383.32
Ursus malayanus	ZMB_Mam_28472	235	97’624.11	400	414.4
Ursus malayanus	ZMUZH 10161	190	63’545.13	330	341.88
Ursus malayanus	ZMUZH 13810	210	77’782.69	330	341.88
Ursus malayanus	ZMUZH 13116	235	97’624.11	350	362.6

Ursus malayanus	ZMUZH 10160	210	77’782.69	340	352.24
Ursus malayanus	NMBE 1042692	183	58’904.87	260	269.36
Ursus malayanus	NMBE 1042688	238	100’157.96	310	321.16
Ursus malayanus	NMBE 1042689	206	74’818.98	260	269.36
Ursus malayanus	NMBE 1042684	183	58’904.87	250	259
Ursus malayanus	NMBE 1042677	182	58’256.48	250	259
Ursus malayanus	NBC 4103	217	83’109.12	300	310.8
Ursus malayanus	RN 11976 (NBC)	205	74’087.13	300	310.8
Ursus malayanus	ZMA 1031 (NBC)	248	108’840.97	390	404.04
Ursus malayanus	ZMA 14039 (NBC)	244	105’324.03	360	372.96
Ursus malayanus	ZMA 1028 (NBC)	248	108’840.97	370	383.32
Ursus malayanus	ZMA 1027 (NBC)	209	77’036.31	310	321.16
Ursus malayanus	ZMA 9083 (NBC)	219	84’663.67	310	321.16
Ursus malayanus	ZMA 9084 (NBC)	226	90’219.22	420	435.12
Ursus malayanus	ZMA 9085 (NBC)	212	79’286.35	350	362.6
Ursus malayanus	ZMA 23321 (NBC)	231	94’296.64	320	331.52
Ursus malayanus	RN 12212 (NBC)	179	56’333.03	260	269.36
Ursus malayanus	RN 679 (NBC)	182	58’256.48	220	227.92
Ursus malayanus	RN 2298 (NBC)	202	71’913.39	340	352.24
Ursus malayanus	RN 2628 (NBC)	233	95’953.09	370	383.32
Ursus malayanus	RN 4878 (NBC)	239	101’009.86	420	435.12
Ursus malayanus	RN 252 (NBC)	239	101’009.86	380	393.68
Ursus malayanus	RN F152 (NBC)	214	80’804.55	360	372.96
Ursus malayanus	RN 907 (NBC)	209	77’036.31	320	331.52
Ursus malayanus	RN 3320 (NBC)	217	83’109.12	390	404.04
Ursus malayanus	RN 1 (NBC)	221	86’232.78	320	331.52
Ursus malayanus	NBC no nmb	225	89’414.65	330	341.88
Ursus malayanus	NBC no nmb	225	89’414.65	350	362.6
Ursus malayanus	MNHN 1919-62	221	86’232.78	350	362.6
Ursus malayanus	MNHN 2006-413	204	73’358.92	320	331.52
Ursus malayanus	MNHN 1936-398	211	78’532.71	320	331.52
Ursus malayanus	MNHN A 2132	228	91’839.26	340	352.24
Ursus malayanus	MNHN 2006-443	219	84’663.67	320	331.52
Ursus malayanus	MNHN 2005-708	209	77’036.31	350	362.6
Ursus malayanus	MNHN 1914-360	212	79’286.35	320	331.52
Ursus malayanus	MNHN no nmb	184	59’556.89	250	259
Ursus maritimus	ZMB_Mam_14384	367	240’229.01	550	569.8
Ursus maritimus	ZMB_Mam_14385	382	260’476.17	540	559.44
Ursus maritimus	ZMB_Mam_14383	317	178’706.24	470	486.92
Ursus maritimus	ZMB_Mam_18700	338	203’428.47	470	486.92
Ursus maritimus	ZMB_Mam_18702	334	198’594.80	450	466.2
Ursus maritimus	ZMB_Mam_18693	328	191’454.32	500	518
Ursus maritimus	ZMB_Mam_18695	361	232’361.70	520	538.72
Ursus maritimus	ZMB_Mam_18698	358	228’477.65	490	507.64
Ursus maritimus	ZMB_Mam_18692	334	198’594.80	470	486.92
Ursus maritimus	ZMB_Mam_18697	336	201’004.30	460	476.56
Ursus maritimus	ZMB_Mam_18691	364	236’278.82	520	538.72
Ursus maritimus	ZMB_Mam_18696	324	186’767.33	480	497.28
Ursus maritimus	ZMB_Mam_18706	333	197’395.55	500	518
Ursus maritimus	ZMB_Mam_18712	298	157’730.93	400	414.4
Ursus maritimus	ZMB_Mam_18703	382	260’476.17	590	611.24

Ursus maritimus	ZMB_Mam_18704	382	260’476.17	570	590.52
Ursus maritimus	ZMB_Mam_29544	364	236’278.82	540	559.44
Ursus maritimus	ZMB_Mam_18716	354	223’350.33	510	528.36
Ursus maritimus	ZMB_Mam_18713	300	159’876.61	480	497.28
Ursus maritimus	ZMB_Mam_29543	329	192’635.23	440	455.84
Ursus maritimus	ZMB_Mam_18729	371	245’547.38	520	538.72
Ursus maritimus	ZMB_Mam_43704	363	234’969.44	580	600.88
Ursus maritimus	ZMB_Mam_43703	343	209’553.12	470	486.92
Ursus maritimus	ZMB_Mam_43702	375	250’924.55	550	569.8
Ursus maritimus	ZMB_Mam_29542	321	183’290.59	430	445.48
Ursus maritimus	ZMB_Mam_43719	337	202’214.55	450	466.2
Ursus maritimus	ZMB_Mam_43714	323	185’604.75	440	455.84
Ursus maritimus	ZMB_Mam_43717	317	178’706.24	460	476.56
Ursus maritimus	ZMB_Mam_43707	366	238’908.61	550	569.8
Ursus maritimus	ZMB_Mam_43706	332	196’199.97	450	466.2
Ursus maritimus	ZMB_Mam_43716	334	198’594.80	480	497.28
Ursus maritimus	ZMB_Mam_43705	373	248’228.61	550	569.8
Ursus maritimus	ZMB_Mam_43710	352	220’808.70	500	518
Ursus maritimus	ZMB_Mam_48803	357	227’190.31	580	600.88
Ursus maritimus	ZMB_Mam_69373	388	268’806.70	550	569.8
Ursus maritimus	ZMB_Mam_69375	318	179’846.83	430	445.48
Ursus maritimus	ZMB_Mam_46573	383	261’855.39	540	559.44
Ursus maritimus	ZMB_Mam_48691	314	175’306.45	440	455.84
Ursus maritimus	ZMB_Mam_69374	374	249’574.75	520	538.72
Ursus maritimus	ZMB_Mam_83387	394	277’269.67	540	559.44
Ursus maritimus	ZMUZH 10313	331	195’008.05	460	476.56
Ursus maritimus	ZMUZH 10309	314	175’306.45	410	424.76
Ursus maritimus	PIMUZ 13129	372	246’886.16	510	528.36
Ursus maritimus	RN 2197 (NBC)	363	234’969.44	540	559.44
Ursus maritimus	Rn cat. d. (NBC)	376	252’278.04	480	497.28
Ursus maritimus	Rn cat. c. (NBC)	374	249’574.75	500	518
Ursus maritimus	Rn cat. b. (NBC)	365	237’591.88	500	518
Ursus maritimus	RN 20384 (NBC)	378	254’996.04	530	549.08
Ursus maritimus	RN 20385 (NBC)	326	189’103.49	420	435.12
Ursus maritimus	RN 20386 (NBC)	326	189’103.49	410	424.76
Ursus maritimus	RN 20381 (NBC)	331	195’008.05	430	445.48
Ursus maritimus	ZMA 22185 (NBC)	300	159’876.61	410	424.76
Ursus maritimus	ZMA 1009 (NBC)	357	227’190.31	510	528.36
Ursus maritimus	ZMA 2585 (NBC)	300	159’876.61	380	393.68
Ursus maritimus	NBC 21701	323	185’604.75	410	424.76
Ursus maritimus	NBC 21700	387	267’409.08	540	559.44
Ursus maritimus	RN 20387 (NBC)	342	208’320.85	460	476.56
Ursus maritimus	ZAM 25156 (NBC)	334	198’594.80	410	424.76
Ursus maritimus	ZAM 19653 (NBC)	321	183’290.59	460	476.56
Ursus maritimus	RN 20383 (NBC)	381	259’100.62	490	507.64
Ursus maritimus	RN 19774 (NBC)	373	248’228.61	540	559.44
Ursus maritimus	RN 19772 (NBC)	326	189’103.49	470	486.92
Ursus maritimus	21699 (NBC)	381	259’100.62	540	559.44
Ursus maritimus	RN 20382 (NBC)	333	197’395.55	420	435.12
Ursus maritimus	RN 19773 (NBC)	304	164’211.90	400	414.4
Ursus maritimus	ZAM 17546 (NBC)	379	256’360.56	460	476.56

Ursus maritimus	MNHN 1943-51	357	227’190.31	490	507.64
Ursus maritimus	MNHN 1938-93	331	195’008.05	490	507.64
Ursus maritimus	MNHN 1934-50	308	168’605.78	400	414.4
Ursus maritimus	MNHN 1996-2172	327	190’277.07	410	424.76
Ursus maritimus	MNHN 1985-1874	320	182’139.00	500	518
Ursus maritimus	MNHN 1934-51	318	179’846.83	460	476.56
Ursus maritimus	MNHN 1972-620	312	173’058.24	490	507.64
Ursus maritimus	MNHN 1906-57	358	228’477.65	490	507.64
Ursus maritimus	MNHN 1928-300	320	182’139.00	420	435.12
Ursus maritimus	MNHN 1928-299	285	144’140.70	400	414.4
Ursus maritimus	MNHN 1928-304	314	175’306.45	450	466.2
Ursus maritimus	MNHN 1865-168	376	252’278.04	570	590.52
Ursus maritimus	MNHN 1971-266	320	182’139.00	430	445.48
Ursus maritimus	MNHN 1928-316	325	187’933.58	460	476.56
Ursus maritimus	MNHN 1929-218	328	191’454.32	520	538.72
Ursus maritimus	MNHN 1961-293	337	202’214.55	430	445.48
Ursus spelaeus	Arnsteinhöhle bei Meyerling, A 5547	454	369’192.46	420	435.12
Ursus spelaeus	Conturines, Cu 703	386	266’015.14	420	435.12
Ursus spelaeus	Drachenloch 1	436	340’222.25	450	466.2
Ursus spelaeus	Drachenloch 10	390	271’612.97	370	383.32
Ursus spelaeus	Drachenloch 11	379	256’360.56	350	362.6
Ursus spelaeus	Drachenloch 13	374	249’574.75	420	435.12
Ursus spelaeus	Drachenloch 20	362	233’663.73	310	321.16
Ursus spelaeus	Drachenloch 21	357	227’190.31	360	372.96
Ursus spelaeus	Drachenloch 3	387	267’409.08	450	466.2
Ursus spelaeus	Drachenloch 4	425	323’106.46	440	455.84
Ursus spelaeus	Drachenloch, no nmb	428	327’730.16	410	424.76
Ursus spelaeus	Gamssulzen GS 524	441	348’149.64	380	393.68
Ursus spelaeus	Gamssulzen, 1926/392	-	-	410	424.76
Ursus spelaeus	Jgritzer Höhle bei Elesd, A 5332	465	387’485.06	500	518
Ursus spelaeus	Krzna Jama, A5335	366	238’908.61	320	331.52
Ursus spelaeus	Krzna Jama, no nmb	448	359’402.91	430	445.48
Ursus spelaeus	Medveda Dvorona x	366	238’908.61	400	414.4
Ursus spelaeus	Medvedina Jama, Mj 980	479	411’412.74	470	486.92
Ursus spelaeus	Medvedja Jama 71	433	335’510.06	390	404.04
Ursus spelaeus	Merkensteinhöhle, no nmb	386	266’015.14	330	341.88
Ursus spelaeus	Mixnitz 10	476	406’224.44	440	455.84
Ursus spelaeus	Mixnitz 12	465	387’485.06	460	476.56
Ursus spelaeus	Mixnitz 14	462	382’451.87	400	414.4
Ursus spelaeus	Mixnitz 15	459	377’451.91	450	466.2
Ursus spelaeus	Mixnitz 20	361	232’361.70	360	372.96
Ursus spelaeus	Mixnitz 21	454	369’192.46	410	424.76
Ursus spelaeus	Mixnitz 22	449	361’025.28	480	497.28
Ursus spelaeus	Mixnitz 30	433	335’510.06	390	404.04
Ursus spelaeus	Mixnitz 3000/3/25	385	264’624.88	420	435.12
Ursus spelaeus	Mixnitz 3000/3/31	487	425’410.79	510	528.36
Ursus spelaeus	Mixnitz 3000/3/32	435	338’647.83	470	486.92
Ursus spelaeus	Mixnitz 3000/3/33	442	349’746.18	390	404.04
Ursus spelaeus	Mixnitz 3000/3/34	427	326’185.24	430	445.48
Ursus spelaeus	Mixnitz 3000/3/37	454	369’192.46	450	466.2

Ursus spelaeus	Mixnitz 3000/3/4	396	280’120.10	360	372.96
Ursus spelaeus	Mixnitz 3000/3/44	404	291’669.06	400	414.4
Ursus spelaeus	Mixnitz 3000/3/5	414	306’436.64	420	435.12
Ursus spelaeus	Mixnitz 3000/3/6	475	404’502.39	480	497.28
Ursus spelaeus	Mixnitz 3003/3/36	427	326’185.24	450	466.2
Ursus spelaeus	Mixnitz 3003/3/39	399	284’423.35	350	362.6
Ursus spelaeus	Mixnitz 3003/3/43	407	296’060.66	370	383.32
Ursus spelaeus	Mixnitz 31	443	351’346.42	480	497.28
Ursus spelaeus	Mixnitz 38	423	320’042.42	350	362.6
Ursus spelaeus	Mixnitz 41	419	313’958.56	420	435.12
Ursus spelaeus	Mixnitz 45	391	273’021.63	360	372.96
Ursus spelaeus	Mixnitz 48	375	250’924.55	390	404.04
Ursus spelaeus	Mixnitz 5	475	404’502.39	460	476.56
Ursus spelaeus	Mixnitz 50	363	234’969.44	350	362.6
Ursus spelaeus	Mixnitz 7	474	402’784.04	410	424.76
Ursus spelaeus	Mixnitz 90	370	244’212.27	400	414.4
Ursus spelaeus	Mixnitz 90	454	369’192.46	420	435.12
Ursus spelaeus	Mixnitz F 14	450	362’651.33	390	404.04
Ursus spelaeus	Mixnitz Sch90	364	236’278.82	380	393.68
Ursus spelaeus	Petralona, PEC 1000	454	369’192.46	550	569.8
Ursus spelaeus	Salzofenhöhle 2724	406	294’593.11	440	455.84
Ursus spelaeus	Salzofenhöhle, no nmb	440	346’556.79	410	424.76
Ursus spelaeus	Salzofenhöhle, no nmb	378	254’996.04	430	445.48
Ursus spelaeus	Salzofenhöhle, Q3/23	390	271’612.97	370	383.32
Ursus spelaeus	Salzofenhöhle, Q4/1	390	271’612.97	390	404.04
Ursus spelaeus	Salzofenhöhle, RZ IX 1963	445	354’557.95	480	497.28
Ursus spelaeus	Salzofenhöhle, RZ XI 1963	410	300’485.41	410	424.76
Ursus spelaeus	Salzofenhöhle, SH 53	449	361’025.28	510	528.36
Ursus spelaeus	Salzofenhöhle, SH 62	366	238’908.61	330	341.88
Ursus spelaeus	Salzofenhöhle, SH 62	415	307’933.65	420	435.12
Ursus spelaeus	Schreiberwandhöhle, SR 112	421	316’993.12	430	445.48
Ursus spelaeus	Schwabenreith, SW 185c	418	312’446.81	360	372.96
Ursus spelaeus	Schwabenreith, SW 2052	423	320’042.42	420	435.12
Ursus spelaeus	Schwabenreith, SW 457	378	254’996.04	390	404.04
Ursus spelaeus	Schwabenreith, SW 483	432	333’946.71	440	455.84
Ursus spelaeus	Schwabenreith, SW 512	437	341’800.35	400	414.4
Ursus spelaeus	Schwabenreith, SW 779c	403	290’212.55	420	435.12
Ursus spelaeus	Schwabenreith, SW 849c	391	273’021.63	370	383.32
Ursus spelaeus	Sloupsko-šošůvské jeskyně 70	487	425’410.79	500	518
Ursus spelaeus	Sloupsko-šošůvské jeskyně C 1006	398	282’985.25	370	383.32
Ursus spelaeus	Sloupsko-šošůvské jeskyně, A 5318	470	395’947.56	500	518
Ursus spelaeus	Sloupsko-šošůvské jeskyně, A 5326	469	394’247.68	420	435.12
Ursus spelaeus	Sloupsko-šošůvské jeskyně, A 5329	481	414’890.08	470	486.92
Ursus spelaeus	Sloupsko-šošůvské jeskyně, A 5329	419	313’958.56	370	383.32
Ursus spelaeus	Sloupsko-šošůvské jeskyně, A 5331	424	321’572.60	400	414.4
Ursus spelaeus	Sloupsko-šošůvské jeskyně, A 5543	343	209’553.12	330	341.88

Ursus spelaeus	Sloupsko-šošůvské jeskyně, A 5544	474	402’784.04	500	518
Ursus spelaeus	Sloupsko-šošůvské jeskyně, A 5545	461	380’781.53	430	445.48
Ursus spelaeus	Sloupsko-šošůvské jeskyně, A 5550	374	249’574.75	330	341.88
Ursus spelaeus	Sloupsko-šošůvské jeskyně, A 5552	372	246’886.16	420	435.12
Ursus spelaeus	Sloupsko-šošůvské jeskyně, A 5553	397	281’550.84	360	372.96
Ursus spelaeus	Sloupsko-šošůvské jeskyně, D 4198	484	420’133.81	370	383.32
Ursus spelaeus	Sloupsko-šošůvské jeskyně, D 4204	422	318’515.93	380	393.68
Ursus spelaeus	Sloupsko-šošůvské jeskyně, D 4207	457	374’137.06	430	445.48
Ursus spelaeus	Sloupsko-šošůvské jeskyně, No 2	448	359’402.91	440	455.84
Ursus spelaeus	Sloupsko-šošůvské jeskyně, no nmb	459	377’451.91	500	518
Ursus spelaeus	Sloupsko-šošůvské jeskyně, SL 9	456	372’485.17	450	466.2
Ursus spelaeus	Sundwig, MB. Ma. 5019	439	344’967.62	450	466.2
Ursus spelaeus	Sundwig, St 18445	451	364’281.08	490	507.64
Ursus spelaeus	Vypustekhöhle 1818	468	392’551.48	440	455.84
Ursus spelaeus	Winden, 2678	477	407’950.18	500	518
Ursus spelaeus	Zoolithenhöhle, MB. Ma. 1998	385	264’624.88	350	362.6
Ursus spelaeus	Zoolithenhöhle, MB. Ma. 5017	416	309’434.35	450	466.2
Ursus spelaeus	Zoolithenhöhle, MB. Ma. 5020	462	382’451.87	460	476.56
Ursus spelaeus	Zoolithenhöhle, MB. Ma. 5022	391	273’021.63	350	362.6
Ursus spelaeus	Zoolithenhöhle?, MB. Ma. 2029	382	260’476.17	350	362.6
Ursus thibetanus	ZMB_Mam_17530	288	147’222.04	330	341.88
Ursus thibetanus	ZMB_Mam_69379	236	98’465.08	260	269.36
Ursus thibetanus	ZMB_Mam_69383	236	98’465.08	250	259
Ursus thibetanus	ZMB_Mam_44367	216	82’337.29	180	186.48
Ursus thibetanus	ZMB_Mam_69380	211	78’532.71	230	238.28
Ursus thibetanus	ZMB_Mam_56747	243	104’453.90	270	279.72
Ursus thibetanus	ZMB_Mam_87049	220	85’446.41	230	238.28
Ursus thibetanus	ZMB_Mam_87043	250	110’621.32	250	259
Ursus thibetanus	ZMB_Mam_87096	212	79’286.35	260	269.36
Ursus thibetanus	ZMB_Mam_87050	306	166’401.52	310	321.16
Ursus thibetanus	ZMB_Mam_69399	267	126’343.45	270	279.72
Ursus thibetanus	ZMB_Mam_69396	252	112’416.25	250	259
Ursus thibetanus	ZMB_Mam_69401	247	107’956.26	270	279.72
Ursus thibetanus	NMBE 1042650	252	112’416.25	230	238.28
Ursus thibetanus	NMBE 1042743	264	123’492.32	250	259
Ursus thibetanus	R. Cat. a. (NBC)	296	155’599.88	360	372.96
Ursus thibetanus	ZAM 11689 (NBC)	273	132’144.33	300	310.8
Ursus thibetanus	ZAM 9082 (NBC)	250	110’621.32	240	248.64
Ursus thibetanus	ZAM 14038 (NBC)	258	117’888.60	260	269.36
Ursus thibetanus	ZAM 1026 (NBC)	257	116’967.42	270	279.72
Ursus thibetanus	ZAM 9222 (NBC)	249	109’729.32	290	300.44
Ursus thibetanus	R. Cat. c. (NBC)	263	122’549.24	240	248.64
Ursus thibetanus	RN 4126 (NBC)	256	116’049.89	300	310.8

Ursus thibetanus	MNHN 1964-244	215	81’569.10	280	290.08
Ursus thibetanus	MNHN 2006-419	263	122’549.24	260	269.36
Ursus thibetanus	MNHN 1986-345	252	112’416.25	330	341.88
Ursus thibetanus	MNHN 1870-533	248	108’840.97	300	310.8
Ursus thibetanus	MNHN 2005-415	252	112’416.25	240	248.64
Ursus thibetanus	MNHN 1979-60	277	136’084.65	400	414.4
Ursus ursinus	ZMB_Mam_70510	290	149’294.55	270	279.72
Ursus ursinus	ZMB_Mam_15579	309	169’713.40	300	310.8
Ursus ursinus	ZMB_Mam_45074	301	160’954.94	300	310.8
Ursus ursinus	ZMB_Mam_56748	301	160’954.94	270	279.72
Ursus ursinus	ZMB_Mam_87142	304	164’211.90	300	310.8
Ursus ursinus	ZMB_Mam_13384	285	144’140.70	280	290.08
Ursus ursinus	ZMUZH 13260	267	126’343.45	300	310.8
Ursus ursinus	NMBE 1042812	265	124’439.04	240	248.64
Ursus ursinus	NMBE 1039369	277	136’084.65	260	269.36
Ursus ursinus	ZAM 1025 (NBC)	295	154’539.84	320	331.52
Ursus ursinus	ZMUZH 885	267	126’343.45	270	279.72
Ursus ursinus	ZAM 20465 (NBC)	274	133’123.93	270	279.72
Ursus ursinus	RN 2444 (NBC)	301	160’954.94	280	290.08
Ursus ursinus	RN 2418 (NBC)	269	128’262.47	280	290.08
Ursus ursinus	RN 345 (NBC)	292	151’381.69	250	259
Ursus ursinus	MNHN 2006-559	321	183’290.59	340	352.24
Ursus ursinus	MNHN 1883-59	267	126’343.45	270	279.72

Additional file 2: Table S2. Data subset of brain volume estimates based on external measurements by Finarelli [74] and glass bead method. (XLSX 12 kb)

Species	Cat No	W (mm)	L (mm)	H (mm)	Finarelli 2006 (ml Brain Volume)	Glass Beads (ml Brain Volume)
Ursus malayanus	NMBE 1042677	83	121	55	144	250
Ursus malayanus	NMBE 1042684	87	133	57	163	250
Ursus malayanus	NMBE 1042688	95	163	67	230	310
Ursus malayanus	NMBE 1042689	88	144	56	166	260
Ursus malayanus	NMBE 1042692	88	130	51	146	260
Ursus malayanus	ZMUZH 10160	99	156	61	216	340
Ursus malayanus	ZMUZH 10161	100	142	55	191	330
Ursus malayanus	ZMUZH 13116	108	164	63	254	350
Ursus malayanus	ZMUZH 13810	96	155	57	193	330
Ursus arctos	NMBE 1030173	100	200	86	338	430
Ursus arctos	NMBE 1030241	100	219	89	360	460
Ursus arctos	NMBE 1042343	109	240	103	481	420
Ursus arctos	NMBE 1042355	96	178	72	257	340
Ursus arctos	NMBE 1042361	95	158	70	238	330
Ursus arctos	NMBE 1042363	94	167	69	235	340
Ursus arctos	NMBE 1042364	95	191	82	297	420
Ursus arctos	NMBE 1042366	101	177	80	307	410
Ursus arctos	NMBE 1042369	102	212	93	383	380
Ursus arctos	NMBE 1042372	96	158	69	238	300
Ursus arctos	NMBE 1042374	98	176	74	271	350
Ursus arctos	NMBE 1042376	108	200	89	387	390
Ursus arctos	NMBE 1042379	107	221	85	374	410
Ursus arctos	NMBE 1042381	101	181	93	362	360
Ursus arctos	NMBE 1042383	98	197	86	328	370
Ursus arctos	NMBE 1042384	95	167	77	268	340
Ursus arctos	NMBE 1042390	93	168	75	254	310
Ursus arctos	NMBE 1042393	101	185	79	306	410
Ursus arctos	NMBE 1042394	104	186	79	318	420
Ursus arctos	NMBE 1042395	105	214	89	380	420
Ursus arctos	NMBE 1042396	99	170	81	299	390
Ursus arctos	NMBE 1042399	91	168	68	223	310
Ursus arctos	NMBE 1042410	108	214	89	394	490
Ursus arctos	NMBE 1042414	105	209	88	373	360
Ursus arctos	NMBE 1042417	102	185	78	306	360
Ursus arctos	NMBE 1042418	122	224	104	550	400
Ursus arctos	NMBE 1042426	94	171	71	244	350
Ursus arctos	NMBE 1042563	93	162	61	202	260
Ursus arctos	NMBE 1047854	98	164	70	251	320
Ursus arctos	NMBE 1054620	100	181	71	268	380
Ursus arctos	NMBE 1054621	116	236	85	422	400
Ursus arctos	ZMUZH 10158	105	193	80	330	370
Ursus arctos	ZMUZH 10310	104	182	85	342	350
Ursus arctos syriacus	NMBE 1042413	100	218	91	368	370
Ursus spelaeus	Drachenloch 1	118	268	111	594	450
Ursus spelaeus	Drachenloch 10	112	228	93	440	370
Ursus spelaeus	Drachenloch 11	108	217	92	410	350

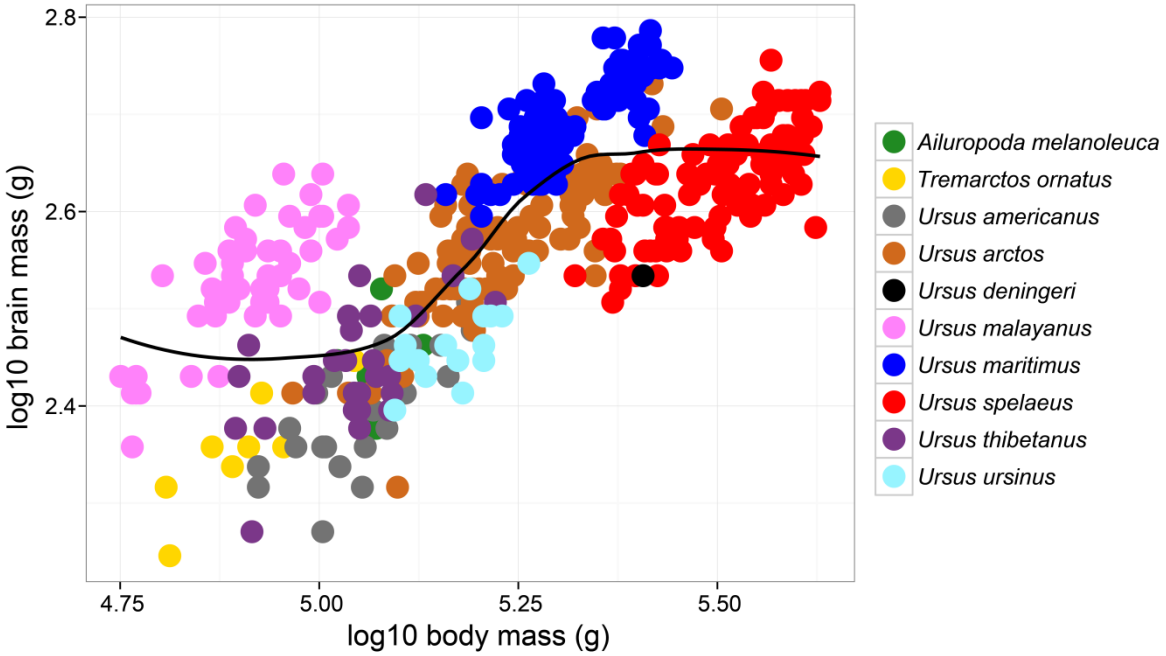
Ursus spelaeus	Drachenloch 13	114	214	95	452	420
Ursus spelaeus	Drachenloch 20	109	211	88	392	310
Ursus spelaeus	Drachenloch 21	108	202	92	402	360
Ursus spelaeus	Drachenloch 3	118	223	103	521	450
Ursus spelaeus	Drachenloch 4	116	247	113	579	440
Ursus spelaeus	Drachenloch No Nmb	111	232	110	523	410
Ursus spelaeus	Petralona, PEC 1000	131	285	113	703	550
Ursus spelaeus	Zoolithenhöhle, MB. Ma. 1998	112	209	97	449	350
Ursus spelaeus	Zoolithenhöhle, MB. Ma. 5017	120	233	105	550	450
Ursus spelaeus	Zoolithenhöhle, MB. Ma. 5020	118	254	110	579	460
Ursus spelaeus	Zoolithenhöhle, MB. Ma. 5022	110	221	104	480	350
Ursus spelaeus	Zoolithenhöhle?, MB. Ma. 2029	110	218	96	439	350

Additional file 3: Supplementary Information. Results for different linear models and corresponding graphical output as well as boxplot on residuals based on PGLS with all species. (PDF 658 kb)

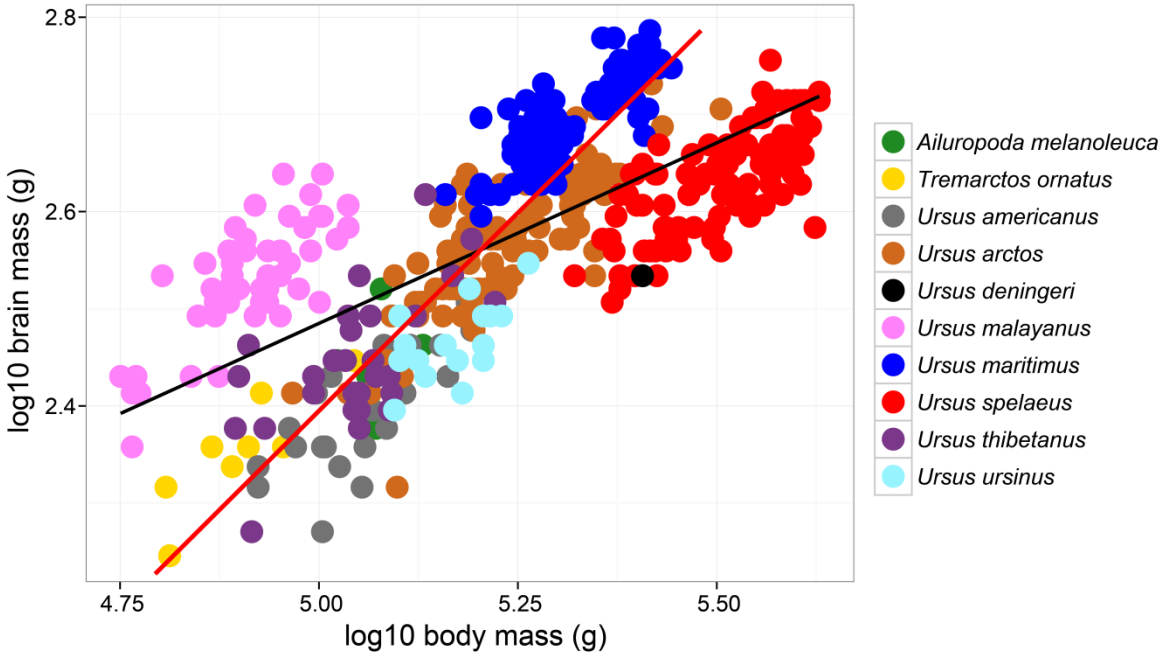
Supplementary Information: The effect of body size evolution and ecology on encephalization in cave bears and extant relatives (Kristof Veitschegger)

Supplementary Table 4: Results of the different linear models investigated in this study.

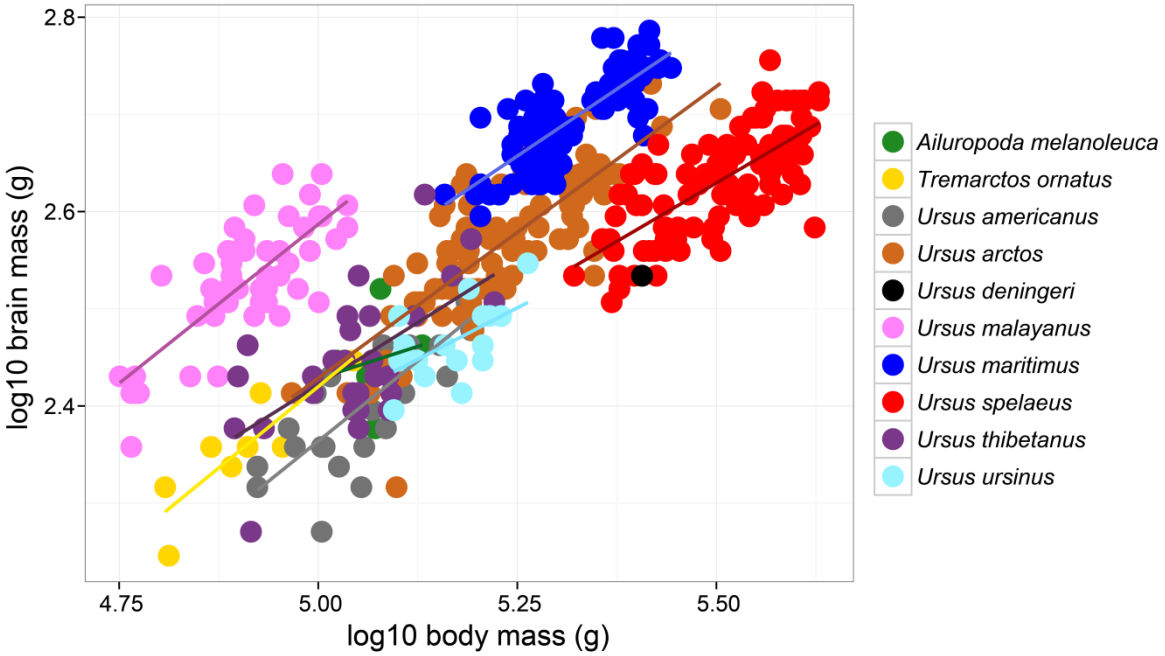
Model	Intercept	Std. Error	t	p	Slope	Std. Error	t	p	multiple R2	adjusted R2
OLS (individual datapoints)	0.6268	0.0946	6.6250	**<0.0001**	0.3716	0.0180	20.6070	**<0.0001**	0.5088	0.5076
OLS (individual datapoints), without *Ursus malayanus* and *Ursus spelaeus*	-1.6605	0.1274	-13.0400	**<0.0001**	0.8113	0.0245	33.1700	**<0.0001**	0.8089	0.8081
PGLS	0.2462	0.7039	0.3498	0.7368	0.4398	0.1370	3.2108	**0.0148**	0.5956	0.5378
PGLS, without *Ursus malayanus* and *Ursus spelaeus*	-1.5100	0.6477	-2.3314	0.0671	0.7807	0.1266	6.1678	**0.0016**	0.8838	0.8606



Supplementary Figure 1: Scatterplot of log10 brain mass (g) against log10 body mass (g) with a LOESS curve (local polynomial regression). Note that *Ursus malayanus* and *Ursus spelaeus* heavily skew the line in opposite directions, thus introducing bias to the linear model. Other bear species fall on one line.



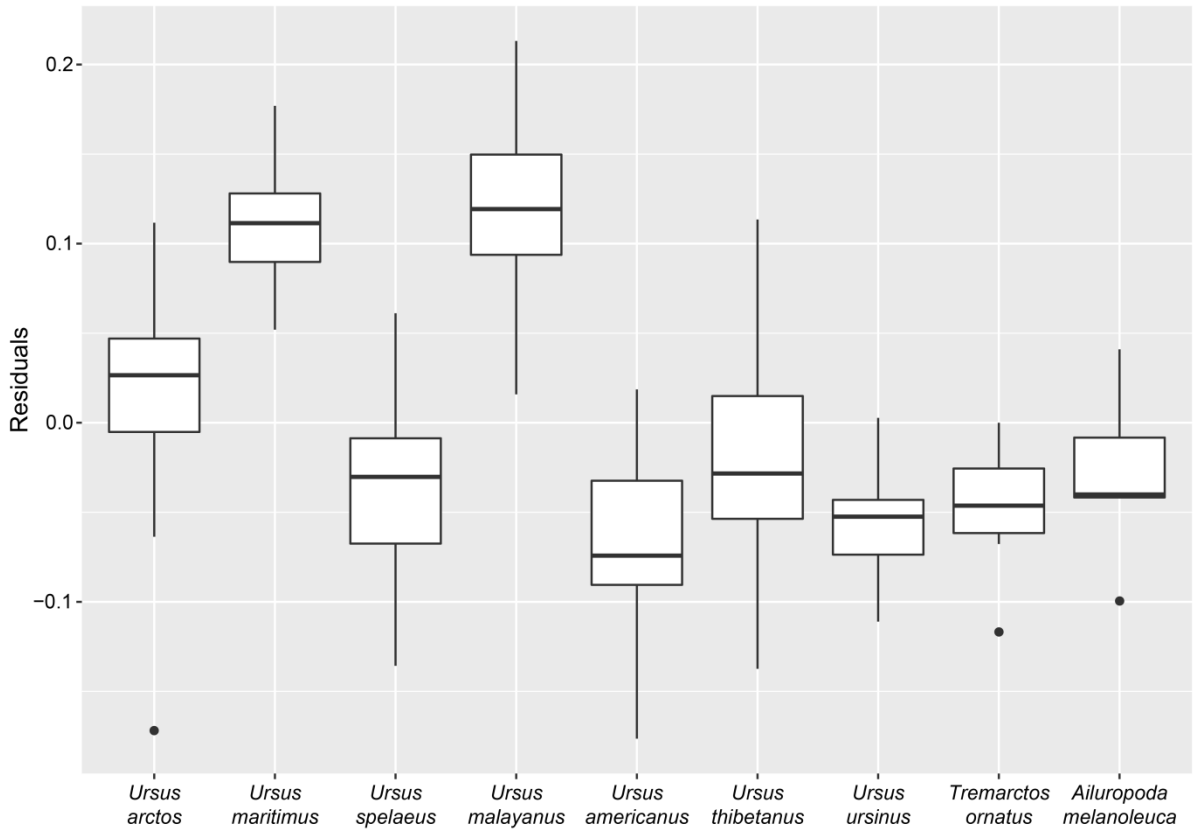
Supplementary Figure 2: Scatterplot of log10 brain mass (g) against log10 body mass (g) with a OLS regression lines (ordinary least squares). In black is the OLS regression line for all data points, in red the OLS regression line without *Ursus malayanus* and *Ursus spelaeus.* (details in Supplementary Table 4)



Supplementary Figure 3: Scatterplot of log10 brain mass (g) against log10 body mass (g) with OLS regression lines (ordinary least squares) for each species.

Supplementary Table 5: Slopes and intercepts based on OLS for all bear species as presented in Supplementary Figure 3.

Model	Intercept	Std. Error	t	p	Slope	Std. Error	t	p	multiple R2	adjusted R2
Ailuropoda melanoleuca	1.1051	3.8413	0.2880	0.7920	0.2646	0.7572	0.3490	0.7500	0.0391	-0.2812
Tremarctos ornatus	-0.9296	0.7951	-1.1690	0.2867	0.6699	0.1622	4.1300	**0.0061**	0.7398	0.6965
Ursus americanus	-0.9378	0.5494	-1.7070	0.0997	0.6603	0.1085	6.0850	**<0.0001**	0.5875	0.5716
Ursus arctos	-0.5754	0.2382	-2.4160	**0.0177**	0.6008	0.0455	13.2160	**<0.0001**	0.6575	0.6537
Ursus malayanus	-0.6836	0.3712	-1.8420	0.0717	0.6541	0.0756	8.6520	**<0.0001**	0.6093	0.6012
Ursus maritimus	-0.2354	0.2416	-0.9740	0.3330	0.5510	0.0454	12.1300	**<0.0001**	0.6478	0.6434
Ursus spelaeus	-0.0146	0.2652	-0.0550	0.9560	0.4807	0.0482	9.9750	**<0.0001**	0.5064	0.5013
Ursus thibetanus	-0.1497	0.6304	-0.2370	0.8141	0.5143	0.1249	4.1180	**0.0003**	0.3858	0.3630
Ursus ursinus	0.2687	0.7664	0.3510	0.7308	0.4252	0.1484	2.8650	**0.0118**	0.3537	0.3106



Supplementary Figure 4: Distribution of residuals based on PGLS (phylogenetic generalized least squares) on all species. Note the higher values for *Ursus spelaeus* compared to the main analysis.

Additional file 4: Table S3. Additional results for slope and intercept pairwise comparisons. (XLSX 31 kb)

Comparison slopes based on *Ailuropoda melanoleuca*

log10brain_mass(g)~log10body_mass(g)*Species	**Estimate**	**Std. Error**	**t-value**	**p-value**
(Intercept)	1.105	2.556	0.432	0.666
log10body_mass(g)	0.265	0.504	0.525	0.600
Tremarctos ornatus	-2.035	2.722	-0.747	0.455
Ursus americanus	-2.043	2.607	-0.784	0.434
Ursus arctos	-1.681	2.566	-0.655	0.513
Ursus malayanus	-1.789	2.583	-0.693	0.489
Ursus maritimus	-1.341	2.579	-0.520	0.603
Ursus spelaeus	-1.120	2.571	-0.435	0.663
Ursus thibetanus	-1.255	2.596	-0.483	0.629
Ursus ursinus	-0.836	2.727	-0.307	0.759
log10body_mass(g):*Tremarctos ornatus*	0.405	0.539	0.752	0.452
log10body_mass(g):*Ursus americanus*	0.396	0.514	0.770	0.442
log10body_mass(g):*Ursus arctos*	0.336	0.506	0.665	0.507
log10body_mass(g):*Ursus malayanus*	0.390	0.509	0.765	0.445
log10body_mass(g):*Ursus maritimus*	0.286	0.508	0.564	0.573
log10body_mass(g):*Ursus spelaeus*	0.216	0.506	0.427	0.670
log10body_mass(g):*Ursus thibetanus*	0.250	0.512	0.488	0.626
log10body_mass(g):*Ursus ursinus*	0.161	0.536	0.299	0.765

Comparison intercepts based on *Ailuropoda melanoleuca*

log10brain_mass(g)~log10body_mass(g)+Species	**Estimate**	**Std. Error**	**t-value**	**p-value**
(Intercept)	-0.420	0.124	-3.376	**0.001**
log10body_mass(g)	0.565	0.024	23.282	**<0.0001**
Tremarctos ornatus	0.003	0.023	0.148	0.882
Ursus americanus	-0.037	0.019	-1.927	0.055
Ursus arctos	0.031	0.018	1.664	0.097
Ursus malayanus	0.173	0.019	9.187	**<0.0001**
Ursus maritimus	0.109	0.019	5.715	**<0.0001**
Ursus spelaeus	-0.060	0.021	-2.875	**0.004**
Ursus thibetanus	0.013	0.019	0.682	0.496
Ursus ursinus	-0.035	0.020	-1.731	0.084

Comparison slopes based on *Tremarctos ornatus*

log10brain_mass(g)~log10body_mass(g)*Species	**Estimate**	**Std. Error**	**t-value**	**p-value**
(Intercept)	-0.930	0.935	-0.994	0.321
log10body_mass(g)	0.670	0.191	3.511	**0.001**
Ailuropoda melanoleuca	2.035	2.722	0.747	0.455
Ursus americanus	-0.008	1.066	-0.008	0.994
Ursus arctos	0.354	0.960	0.369	0.712
Ursus malayanus	0.246	1.005	0.245	0.807
Ursus maritimus	0.694	0.994	0.698	0.486
Ursus spelaeus	0.915	0.975	0.938	0.349
Ursus thibetanus	0.780	1.040	0.750	0.454
Ursus ursinus	1.198	1.333	0.899	0.369
log10body_mass(g):*Ailuropoda melanoleuca*	-0.405	0.539	-0.752	0.452
log10body_mass(g):*Ursus americanus*	-0.010	0.216	-0.044	0.965
log10body_mass(g):*Ursus arctos*	-0.069	0.195	-0.354	0.723
log10body_mass(g):*Ursus malayanus*	-0.016	0.205	-0.077	0.939
log10body_mass(g):*Ursus maritimus*	-0.119	0.201	-0.592	0.554
log10body_mass(g):*Ursus spelaeus*	-0.189	0.197	-0.959	0.338
log10body_mass(g):*Ursus thibetanus*	-0.156	0.211	-0.738	0.461
log10body_mass(g):*Ursus ursinus*	-0.245	0.265	-0.924	0.356

Comparison intercepts based on *Tremarctos ornatus*

log10brain_mass(g)~log10body_mass(g)+Species	**Estimate**	**Std. Error**	**t-value**	**p-value**
(Intercept)	-0.417	0.120	-3.477	**0.001**
log10body_mass(g)	0.565	0.024	23.282	**<0.0001**
Ailuropoda melanoleuca	-0.003	0.023	-0.148	0.882
Ursus americanus	-0.040	0.016	-2.473	**0.014**
Ursus arctos	0.027	0.017	1.646	0.101
Ursus malayanus	0.169	0.015	11.350	**<0.0001**
Ursus maritimus	0.105	0.018	5.947	**<0.0001**
Ursus spelaeus	-0.063	0.020	-3.077	**0.002**
Ursus thibetanus	0.010	0.016	0.598	0.550
Ursus ursinus	-0.038	0.018	-2.119	**0.035**

Comparison slopes based on *Ursus americanus*

log10brain_mass(g)~log10body_mass(g)*Species	**Estimate**	**Std. Error**	**t-value**	**p-value**
(Intercept)	-0.938	0.512	-1.833	0.068
log10body_mass(g)	0.660	0.101	6.535	**<0.0001**
Ailuropoda melanoleuca	2.043	2.607	0.784	0.434
Tremarctos ornatus	0.008	1.066	0.008	0.994
Ursus arctos	0.362	0.555	0.652	0.515
Ursus malayanus	0.254	0.630	0.404	0.687
Ursus maritimus	0.702	0.613	1.146	0.252
Ursus spelaeus	0.923	0.581	1.589	0.113
Ursus thibetanus	0.788	0.684	1.152	0.250
Ursus ursinus	1.206	1.079	1.119	0.264
log10body_mass(g):*Ailuropoda melanoleuca*	-0.396	0.514	-0.770	0.442
log10body_mass(g):*Tremarctos ornatus*	0.010	0.216	0.044	0.965
log10body_mass(g):*Ursus arctos*	-0.060	0.109	-0.545	0.586
log10body_mass(g):*Ursus malayanus*	-0.006	0.126	-0.049	0.961
log10body_mass(g):*Ursus maritimus*	-0.109	0.119	-0.917	0.360
log10body_mass(g):*Ursus spelaeus*	-0.180	0.113	-1.592	0.112
log10body_mass(g):*Ursus thibetanus*	-0.146	0.135	-1.080	0.281
log10body_mass(g):*Ursus ursinus*	-0.235	0.210	-1.121	0.263

Comparison intercepts based on *Ursus americanus*

log10brain_mass(g)~log10body_mass(g)+Species	**Estimate**	**Std. Error**	**t-value**	**p-value**
(Intercept)	-0.457	0.123	-3.708	**0.000**
log10body_mass(g)	0.565	0.024	23.282	**<0.0001**
Ailuropoda melanoleuca	0.037	0.019	1.927	0.055
Tremarctos ornatus	0.040	0.016	2.473	**0.014**
Ursus arctos	0.067	0.009	7.112	**<0.0001**
Ursus malayanus	0.209	0.010	21.009	**<0.0001**
Ursus maritimus	0.145	0.011	13.699	**<0.0001**
Ursus spelaeus	-0.023	0.014	-1.698	0.090
Ursus thibetanus	0.050	0.010	4.776	**<0.0001**
Ursus ursinus	0.002	0.012	0.158	0.875

Comparison slopes based on *Ursus arctos*

log10brain_mass(g)~log10body_mass(g)*Species	**Estimate**	**Std. Error**	**t-value**	**p-value**
(Intercept)	-0.5754	0.2166	-2.6570	**0.0082**
log10body_mass(g)	0.6008	0.0413	14.5330	**<0.0001**
Ailuropoda melanoleuca	1.6805	2.5655	0.6550	0.5128
Tremarctos ornatus	-0.3542	0.9601	-0.3690	0.7124
Ursus americanus	-0.3624	0.5555	-0.6520	0.5145
Ursus malayanus	-0.1082	0.4261	-0.2540	0.7997
Ursus maritimus	0.3400	0.4007	0.8480	0.3967
Ursus spelaeus	0.5608	0.3505	1.6000	0.1104
Ursus thibetanus	0.4257	0.5030	0.8460	0.3979
Ursus ursinus	0.8441	0.9740	0.8670	0.3867
log10body_mass(g):*Ailuropoda melanoleuca*	-0.3362	0.5056	-0.6650	0.5065
log10body_mass(g):*Tremarctos ornatus*	0.0691	0.1952	0.3540	0.7235
log10body_mass(g):*Ursus americanus*	0.0595	0.1092	0.5450	0.5858
log10body_mass(g):*Ursus malayanus*	0.0533	0.0854	0.6240	0.5328
log10body_mass(g):*Ursus maritimus*	-0.0498	0.0757	-0.6580	0.5108
log10body_mass(g):*Ursus spelaeus*	-0.1200	0.0649	-1.8480	0.0653
log10body_mass(g):*Ursus thibetanus*	-0.0865	0.0990	-0.8740	0.3827
log10body_mass(g):*Ursus ursinus*	-0.1756	0.1885	-0.9320	0.3521

Comparison intercepts based on *Ursus arctos*

log10brain_mass(g)~log10body_mass(g)+Species	**Estimate**	**Std. Error**	**t-value**	**p-value**
(Intercept)	-0.3893	0.1272	-3.0600	**0.0024**
log10body_mass(g)	0.5652	0.0243	23.2820	**<0.0001**
Ailuropoda melanoleuca	-0.0306	0.0184	-1.6640	0.0969
Tremarctos ornatus	-0.0273	0.0166	-1.6460	0.1006
Ursus americanus	-0.0672	0.0095	-7.1120	**<0.0001**
Ursus malayanus	0.1419	0.0105	13.4780	**<0.0001**
Ursus maritimus	0.0779	0.0062	12.4760	**<0.0001**
Ursus spelaeus	-0.0903	0.0085	-10.576	**<0.0001**
Ursus thibetanus	-0.0177	0.0095	-1.8570	0.0640
Ursus ursinus	-0.0653	0.0105	-6.2330	**<0.0001**

Comparison slopes based on *Ursus malayanus*

log10brain_mass(g)~log10body_mass(g)*Species	**Estimate**	**Std. Error**	**t-value**	**p-value**
(Intercept)	-0.684	0.367	-1.863	0.063
log10body_mass(g)	0.654	0.075	8.753	**<0.0001**
Ailuropoda melanoleuca	1.789	2.583	0.693	0.489
Tremarctos ornatus	-0.246	1.005	-0.245	0.807
Ursus americanus	-0.254	0.630	-0.404	0.687
Ursus arctos	0.108	0.426	0.254	0.800
Ursus maritimus	0.448	0.498	0.899	0.369
Ursus spelaeus	0.669	0.459	1.458	0.146
Ursus thibetanus	0.534	0.584	0.915	0.361
Ursus ursinus	0.952	1.018	0.935	0.350
log10body_mass(g):*Ailuropoda melanoleuca*	-0.389	0.509	-0.765	0.445
log10body_mass(g):*Tremarctos ornatus*	0.016	0.205	0.077	0.939
log10body_mass(g):*Ursus americanus*	0.006	0.126	0.049	0.961
log10body_mass(g):*Ursus arctos*	-0.053	0.085	-0.624	0.533
log10body_mass(g):*Ursus maritimus*	-0.103	0.098	-1.052	0.293
log10body_mass(g):*Ursus spelaeus*	-0.173	0.090	-1.927	0.055
log10body_mass(g):*Ursus thibetanus*	-0.140	0.117	-1.196	0.233
log10body_mass(g):*Ursus ursinus*	-0.229	0.198	-1.153	0.250

Comparison intercepts based on *Ursus malayanus*

log10brain_mass(g)~log10body_mass(g)+Species	**Estimate**	**Std. Error**	**t-value**	**p-value**
(Intercept)	-0.247	0.119	-2.074	**0.039**
log10body_mass(g)	0.565	0.024	23.282	**<0.0001**
Ailuropoda melanoleuca	-0.173	0.019	-9.187	**<0.0001**
Tremarctos ornatus	-0.169	0.015	-11.350	**<0.0001**
Ursus americanus	-0.209	0.010	-21.009	**<0.0001**
Ursus arctos	-0.142	0.011	-13.478	**<0.0001**
Ursus maritimus	-0.064	0.012	-5.251	**<0.0001**
Ursus spelaeus	-0.232	0.016	-14.599	**<0.0001**
Ursus thibetanus	-0.160	0.010	-16.407	**<0.0001**
Ursus ursinus	-0.207	0.013	-16.431	**<0.0001**

Comparison slopes based on *Ursus maritimus*

log10brain_mass(g)~log10body_mass(g)*Species	**Estimate**	**Std. Error**	**t-value**	**p-value**
(Intercept)	-0.235	0.337	-0.698	0.485
log10body_mass(g)	0.551	0.063	8.693	**<0.0001**
Ailuropoda melanoleuca	1.341	2.579	0.520	0.603
Tremarctos ornatus	-0.694	0.994	-0.698	0.486
Ursus americanus	-0.702	0.613	-1.146	0.252
Ursus arctos	-0.340	0.401	-0.848	0.397
Ursus malayanus	-0.448	0.498	-0.899	0.369
Ursus spelaeus	0.221	0.435	0.507	0.612
Ursus thibetanus	0.086	0.565	0.152	0.880
Ursus ursinus	0.504	1.008	0.500	0.617
log10body_mass(g):*Ailuropoda melanoleuca*	-0.286	0.508	-0.564	0.573
log10body_mass(g):*Tremarctos ornatus*	0.119	0.201	0.592	0.554
log10body_mass(g):*Ursus americanus*	0.109	0.119	0.917	0.360
log10body_mass(g):*Ursus arctos*	0.050	0.076	0.658	0.511
log10body_mass(g):*Ursus malayanus*	0.103	0.098	1.052	0.293
log10body_mass(g):*Ursus spelaeus*	-0.070	0.081	-0.869	0.385
log10body_mass(g):*Ursus thibetanus*	-0.037	0.110	-0.334	0.739
log10body_mass(g):*Ursus ursinus*	-0.126	0.194	-0.647	0.518

Comparison intercepts based on *Ursus maritimus*

log10brain_mass(g)~log10body_mass(g)+Species	**Estimate**	**Std. Error**	**t-value**	**p-value**
(Intercept)	-0.311	0.129	-2.410	**0.016**
log10body_mass(g)	0.565	0.024	23.282	**<0.0001**
Ailuropoda melanoleuca	-0.109	0.019	-5.715	**<0.0001**
Tremarctos ornatus	-0.105	0.018	-5.947	**<0.0001**
Ursus americanus	-0.145	0.011	-13.699	**<0.0001**
Ursus arctos	-0.078	0.006	-12.476	**<0.0001**
Ursus malayanus	0.064	0.012	5.251	**<0.0001**
Ursus spelaeus	-0.168	0.007	-22.940	**<0.0001**
Ursus thibetanus	-0.096	0.011	-8.911	**<0.0001**
Ursus ursinus	-0.143	0.011	-12.919	**<0.0001**

Comparison slopes based on *Ursus spelaeus*

log10brain_mass(g)~log10body_mass(g)*Species	**Estimate**	**Std. Error**	**t-value**	**p-value**
(Intercept)	-0.015	0.276	-0.053	0.958
log10body_mass(g)	0.481	0.050	9.598	**<0.0001**
Ailuropoda melanoleuca	1.120	2.571	0.435	0.663
Tremarctos ornatus	-0.915	0.975	-0.938	0.349
Ursus americanus	-0.923	0.581	-1.589	0.113
Ursus arctos	-0.561	0.351	-1.600	0.110
Ursus malayanus	-0.669	0.459	-1.458	0.146
Ursus maritimus	-0.221	0.435	-0.507	0.612
Ursus thibetanus	-0.135	0.531	-0.254	0.799
Ursus ursinus	0.283	0.989	0.286	0.775
log10body_mass(g):*Ailuropoda melanoleuca*	-0.216	0.506	-0.427	0.670
log10body_mass(g):*Tremarctos ornatus*	0.189	0.197	0.959	0.338
log10body_mass(g):*Ursus americanus*	0.180	0.113	1.592	0.112
log10body_mass(g):*Ursus arctos*	0.120	0.065	1.848	0.065
log10body_mass(g):*Ursus malayanus*	0.173	0.090	1.927	0.055
log10body_mass(g):*Ursus maritimus*	0.070	0.081	0.869	0.385
log10body_mass(g):*Ursus thibetanus*	0.034	0.103	0.326	0.745
log10body_mass(g):*Ursus ursinus*	-0.056	0.191	-0.291	0.771

Comparison intercepts based on *Ursus spelaeus*

log10brain_mass(g)~log10body_mass(g)+Species	**Estimate**	**Std. Error**	**t-value**	**p-value**
(Intercept)	-0.480	0.134	-3.589	**0.000**
log10body_mass(g)	0.565	0.024	23.282	**<0.0001**
Ailuropoda melanoleuca	0.060	0.021	2.875	**0.004**
Tremarctos ornatus	0.063	0.020	3.077	**0.002**
Ursus americanus	0.023	0.014	1.698	0.090
Ursus arctos	0.090	0.009	10.576	**<0.0001**
Ursus malayanus	0.232	0.016	14.599	**<0.0001**
Ursus maritimus	0.168	0.007	22.940	**<0.0001**
Ursus thibetanus	0.073	0.014	5.263	**<0.0001**
Ursus ursinus	0.025	0.013	1.900	0.058

Comparison slopes based on *Ursus thibetanus*

log10brain_mass(g)~log10body_mass(g)*Species	**Estimate**	**Std. Error**	**t-value**	**p-value**
(Intercept)	-0.150	0.454	-0.330	0.742
log10body_mass(g)	0.514	0.090	5.718	**<0.0001**
Ailuropoda melanoleuca	1.255	2.596	0.483	0.629
Tremarctos ornatus	-0.780	1.040	-0.750	0.454
Ursus americanus	-0.788	0.684	-1.152	0.250
Ursus arctos	-0.426	0.503	-0.846	0.398
Ursus malayanus	-0.534	0.584	-0.915	0.361
Ursus maritimus	-0.086	0.565	-0.152	0.880
Ursus spelaeus	0.135	0.531	0.254	0.799
Ursus ursinus	0.418	1.053	0.398	0.691
log10body_mass(g):*Ailuropoda melanoleuca*	-0.250	0.512	-0.488	0.626
log10body_mass(g):*Tremarctos ornatus*	0.156	0.211	0.738	0.461
log10body_mass(g):*Ursus americanus*	0.146	0.135	1.080	0.281
log10body_mass(g):*Ursus arctos*	0.087	0.099	0.874	0.383
log10body_mass(g):*Ursus malayanus*	0.140	0.117	1.196	0.233
log10body_mass(g):*Ursus maritimus*	0.037	0.110	0.334	0.739
log10body_mass(g):*Ursus spelaeus*	-0.034	0.103	-0.326	0.745
log10body_mass(g):*Ursus ursinus*	-0.089	0.205	-0.435	0.664

Comparison intercepts based on *Ursus thibetanus*

log10brain_mass(g)~log10body_mass(g)+Species	**Estimate**	**Std. Error**	**t-value**	**p-value**
(Intercept)	-0.407	0.123	-3.316	**0.001**
log10body_mass(g)	0.565	0.024	23.282	**<0.0001**
Ailuropoda melanoleuca	-0.013	0.019	-0.682	0.496
Tremarctos ornatus	-0.010	0.016	-0.598	0.550
Ursus americanus	-0.050	0.010	-4.776	**<0.0001**
Ursus arctos	0.018	0.010	1.857	0.064
Ursus malayanus	0.160	0.010	16.407	**<0.0001**
Ursus maritimus	0.096	0.011	8.911	**<0.0001**
Ursus spelaeus	-0.073	0.014	-5.263	**<0.0001**
Ursus ursinus	-0.048	0.012	-3.874	**0.000**

Comparison slopes based on *Ursus ursinus*

log10brain_mass(g)~log10body_mass(g)*Species	**Estimate**	**Std. Error**	**t-value**	**p-value**
(Intercept)	0.269	0.950	0.283	0.777
log10body_mass(g)	0.425	0.184	2.312	**0.021**
Ailuropoda melanoleuca	0.836	2.727	0.307	0.759
Tremarctos ornatus	-1.198	1.333	-0.899	0.369
Ursus americanus	-1.206	1.079	-1.119	0.264
Ursus arctos	-0.844	0.974	-0.867	0.387
Ursus malayanus	-0.952	1.018	-0.935	0.350
Ursus maritimus	-0.504	1.008	-0.500	0.617
Ursus spelaeus	-0.283	0.989	-0.286	0.775
Ursus thibetanus	-0.418	1.053	-0.398	0.691
log10body_mass(g):*Ailuropoda melanoleuca*	-0.161	0.536	-0.299	0.765
log10body_mass(g):*Tremarctos ornatus*	0.245	0.265	0.924	0.356
log10body_mass(g):*Ursus americanus*	0.235	0.210	1.121	0.263
log10body_mass(g):*Ursus arctos*	0.176	0.188	0.932	0.352
log10body_mass(g):*Ursus malayanus*	0.229	0.198	1.153	0.250
log10body_mass(g):*Ursus maritimus*	0.126	0.194	0.647	0.518
log10body_mass(g):*Ursus spelaeus*	0.056	0.191	0.291	0.771
log10body_mass(g):*Ursus thibetanus*	0.089	0.205	0.435	0.664

Comparison intercepts based on *Ursus ursinus*

log10brain_mass(g)~log10body_mass(g)+Species	**Estimate**	**Std. Error**	**t-value**	**p-value**
(Intercept)	-0.455	0.126	-3.616	**0.000**
log10body_mass(g)	0.565	0.024	23.282	**<0.0001**
Ailuropoda melanoleuca	0.035	0.020	1.731	0.084
Tremarctos ornatus	0.038	0.018	2.119	**0.035**
Ursus americanus	-0.002	0.012	-0.158	0.875
Ursus arctos	0.065	0.010	6.233	**<0.0001**
Ursus malayanus	0.207	0.013	16.431	**<0.0001**
Ursus maritimus	0.143	0.011	12.919	**<0.0001**
Ursus spelaeus	-0.025	0.013	-1.900	0.058
Ursus thibetanus	0.048	0.012	3.874	**0.000**

Additional file 5: Table S4. Node values for ancestral stage reconstructions. (XLSX 13 kb)

log10 Body mass (g)	Derived	Node	Difference %	Difference %
Ursus maritimus	2.70	2.62	102.80	2.80
Ursus arctos	2.57	2.62	98.08	-1.92
Ursus spelaeus	2.63	2.61	100.71	0.71
U.a+U.m	2.62	2.61	100.40	0.40
Ursus malayanus	2.53	2.50	100.98	0.98
U.a+U.t	2.48	2.50	98.89	-1.11
Ursus thibetanus	2.45	2.48	98.80	-1.20
Ursus americanus	2.41	2.48	97.15	-2.85
U.m+U.a+U.t	2.50	2.51	99.82	-0.18
U.a+U.m+U.s	2.61	2.51	104.14	4.14
U.m+U.a+U.t+U.a+U.m+U.s	2.51	2.49	100.60	0.60
Ursus ursinus	2.46	2.49	98.87	-1.13
U.m+U.a+U.t+U.a+U.m+U.s+U.u	2.49	2.44	102.05	2.05
Tremarctos ornatus	2.35	2.44	96.37	-3.63
U.m+U.a+U.t+U.a+U.m+U.s+U.u+T.o	2.44	2.44	99.98	-0.02
Ailuropoda melanoleuca	2.45	2.44	100.17	0.17

log10 Brain mass (g)	Derived	Node	Difference %	Difference %
Ursus maritimus	5.32	5.30	100.29	0.29
Ursus arctos	5.24	5.30	98.76	-1.24
Ursus spelaeus	5.50	5.33	103.29	3.29
U.a+U.m	5.30	5.33	99.57	-0.43
Ursus malayanus	4.91	5.11	96.09	-3.91
U.a+U.t	5.09	5.11	99.62	-0.38
Ursus thibetanus	5.05	5.09	99.16	-0.84
Ursus americanus	5.06	5.09	99.46	-0.54
U.m+U.a+U.t	5.11	5.12	99.75	-0.25
U.a+U.m+U.s	5.33	5.12	104.00	4.00
U.m+U.a+U.t+U.a+U.m+U.s	5.12	5.12	100.03	0.03
Ursus ursinus	5.16	5.12	100.86	0.86
U.m+U.a+U.t+U.a+U.m+U.s+U.u	5.12	5.05	101.45	1.45
Tremarctos ornatus	4.90	5.05	97.12	-2.88
U.m+U.a+U.t+U.a+U.m+U.s+U.u+T.o	5.05	5.05	99.95	-0.05
Ailuropoda melanoleuca	5.07	5.05	100.46	0.46

Chapter III

Palaeohistology and life history evolution in cave bears, *Ursus spelaeus* s.l.

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Author Contributions:

KV designed and conceived the study, prepared thin sections, collected the data, performed the analyses, prepared the figures and tables, and wrote and reviewed the manuscript.

EA designed and conceived the study and prepared thin sections

CK designed and conceived the study, prepared thin sections, and reviewed the manuscript.

MRSV and TMS designed and conceived the study and reviewed the manuscript.

Palaeohistology and life history evolution in cave bears, *Ursus spelaeus* s.l.

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Abstract

The microstructure of cave bear bones has not received much attention despite its potential to provide crucial information on the biology and life history of this extinct animal. The histological study of 62 femora from 23 different European localities revealed a microstructure characterized by a fibrolamellar complex with an increasing amount of parallel-fibered and lamellar bone towards the outer cortex. Secondary remodelling of the primary bone tissue initially occurs close to the perimedullary margin of the bone cortex around the linea aspera of the femur. In general, a similar histology can be observed in extant bear species. However, secondary remodelling and the composition of the fibrolamellar complex vary greatly. Cave bears grew at a considerably fast pace and reached skeletal maturity between the age of 11 to 14, which is late compared to most other bear species. The sampling included cave bear bones from localities at different altitudes. There is a significant correlation between altitude and growth speed. Based on the reconstructed growth rates, life history theory suggests that cave bears had small offspring and large litter sizes.

Keywords: ontogeny, femora, growth rate, altitude, *Ursus arctos*

Introduction

During the Pleistocene, Eurasia was home to many large sized mammals, commonly referred to as megafauna [1, 2]. A prominent member of this megafauna was the cave bear, *Ursus spelaeus*, one of the most commonly found Pleistocene mammals [3]. Specimens of this species were recovered in numerous Eurasian localities ranging from Spain to Russia [4]. The closest living relatives of *U. spelaeus* are the brown bear, *U. arctos* and the polar bear, *U. maritimus*. The lineage of cave bears split between 2.75 and 1.4 Ma years from the aforementioned two taxa and, early on, underwent a dietary change towards herbivory [5-7]. The hypothesized ancestral species of cave bears, *U. deningeri* [3, 8], had a herbivorous diet [3, 9]. Molecular studies have shown that several distinct haplotype groups of cave bears are recognisable [10-12]. Some authors suggest giving species and subspecies status to some of those, [13] but it remains unclear if species status can be assigned to those cave bear haplotypes [4]. As this is not completely resolved yet, we use *U. spelaeus* sensu lato here, including *U. ingressus*, *U. s. eremus*, and *U. s. ladinicus*.

Cave bears hibernated during Pleistocene winters and therefore spent a considerable amount of the year inactive [14]. Non-hibernating mammals risk losing balance of bone resorption and formation in favour of resorption when being inactive for extended periods, which leads to extensive loss of bone minerals in short time [15]. In extant hibernating bears, however, the balance between resorption and formation is not affected by extended inactive periods but cortical bone turnover rate is lower [16, 17]. The cortical bone geometry and strength of the femoral midshaft remain unchanged [17].

Bone histology of extinct mammals has gained an increased interest in recent years, as details found in thin sections provide insights into the life history of extinct animals [18-23]. These works focus on the growth of different mammalian species by investigating the deposition of different bone tissue types and/or by measuring growth cycles, i.e. by measuring the distance between lines of arrested growth (LAGs) or growth annuli [24]. According to Amprino's rule, different bone tissue types are produced in varying speed [25]. The fastest tissue to be produced is so-called woven-fibered bone, followed by parallel-fibered and lamellar bone [26, 27]. Besides these three, fibrolamellar complex is found in mammals. Here, initially highly vascularised woven-fibered scaffolding is deposited. In a later stage, the mostly reticular or plexiform vascular canals are filled with parallel-fibered and lamellar bone [27]. Recently, the term fibrolamellar complex has come under scrutiny as it does not provide detailed information about formation or structure of primary bone tissue [28]. Nonetheless, we continue using fibrolamellar complex to ensure comparability to previous studies [23]. A LAG is a thin opaque or translucent, circumferential line of compact bone and indicates a cessation of growth [24, 27]. In recent years, evidence has accumulated that the formation of LAGs follows a yearly pattern and that it is independent from

climate or metabolic rate [20, 27, 29-32]. Here, we investigate the histology and growth of cave bears and compare them to those of extant bear species. Based on comprehensive sampling, we examined the variation in growth in the context of geographic location and altitude.

Material and Methods

We investigated 62 femora of cave bears from 23 different localities (Table 1), as well as specimens of one other extinct and of five extant species of the genus *Ursus*. *U. deningeri* is represented by three femora. The sampled femora of extant bear species are those of *U. americanus* (two), *U. arctos* (six), *U. maritimus* (two), *U. malayanus* (one), and *U. ursinus* (one). For *U. spelaeus* and *U. arctos*, ontogenetic series were examined and in case of *U. arctos* the approximate age of three individuals was known (Table 1). The preparation of the thin sections followed standard procedures [19, 22, 33]. The midshaft of the femur was chosen, as it preserves the most information about growth [19, 34]. Growth rates were reconstructed by measuring the distance between consecutive LAGs. The histology of the bones was observed under normal transmitted or cross-polarized light using a Leica DM 2500 M composite microscope. Often, histological details were more pronounced using a lambda compensator. Pictures were taken using a Leica DFC 420 C digital camera. Growth zones were measured using Leica IM 50 Image Manager software.

For statistical assessment of the results, measurements were acquired on the medial part of the femur. The medial part of the bone was chosen because it exhibits the clearest signal (Figure 1). The respective measurements among growth zones 2 to 5 were averaged to compare the growth speed and evenness among species, as these were the common ones to all species. After growth zone five the outer circumferential layer (OCL) is deposited in *U. malayanus*. For the comparison of growth speed and evenness among different localities, growth zones 2 to 7 were averaged, because these were found in all samples. Growth evenness was compared by using standard deviation. We analyzed whether growth speed was correlated with altitude using Kendal's Tau. Statistical analyses were performed in R, version 3.2.3 [35] using the packages ggplot2 [36] and Kendall [37].

Following institutions provided material for sampling: Aristotle University of Thessaloniki - School of Geology (AUTH), Biologiezentrum Linz (BZL), Canadian Museum of Nature (CMN), Finnish Museum of Natural History (MZH), Institut für Paläontologie Universität Erlangen (IPUE), Institut für Paläontologie Universität Wien (PIUW), Museum für Naturkunde Berlin (MfN), Muséum national d'Histoire naturelle (MNHN), Naturhistorisches Museum Basel (NMB), Naturhistorisches Museum Wien (NHM), Naturmuseum Südtirol Bozen (PZO), Naturmuseum St. Gallen (NMSG), Paläontologische Sammlung der Universität Tübingen (GPIT), and Swedish Museum of Natural History (SMNH).

Results

Table 1: Femora examined for this study.

Species	Ontogenetic Stage	Locality	Collection Number
Ursus americanus	adult	-	CMN 41055
Ursus americanus	adult	-	MNHN 1930-208
Ursus arctos	senile	-	MNHN 1904-244
Ursus arctos	adult	-	MZH KN 1358
Ursus arctos	juvenile (<1 y)	Sweden	SMNH 2016-5132
Ursus arctos	subadult	Sweden	SMNH 2016-5131
Ursus arctos	adult (12-15 y)	Sweden	SMNH 2016-5025
Ursus arctos	adult (8-10 y)	Sweden	SMNH 2015-5706
Ursus deningeri	adult	Herkova Jama, Slovenia	HJ 95 (PIUW)
Ursus deningeri	juvenile	Herkova Jama, Slovenia	HJ 151 (PIUW)
Ursus deningeri	juvenile	Herkova Jama, Slovenia	HJ 116 (PIUW)
Ursus malayanus	adult	-	MNHN 1914-360
Ursus maritimus	adult	-	MZH UN 2355
Ursus maritimus	adult	-	MNHN 1835-85
Ursus spelaeus	adult	Arzberghöhle, Austria	Arz 13 (PIUW)
Ursus spelaeus	juvenile	Arzberghöhle, Austria	Arz 24 (PIUW)
Ursus spelaeus	juvenile	Arzberghöhle, Austria	Arz 205 (PIUW)
Ursus spelaeus	adult	Brettsteinbärenhöhle, Austria	BS F1 (PIUW)
Ursus spelaeus	juvenile	Brettsteinbärenhöhle, Austria	BS 36 (PIUW)
Ursus spelaeus	juvenile	Brettsteinbärenhöhle, Austria	BS 134 (PIUW)
Ursus spelaeus	juvenile	Brettsteinbärenhöhle, Austria	BS 43 (PIUW)
Ursus spelaeus	adult	Conturines, Italy	PZO 3852
Ursus spelaeus	adult	Conturines, Italy	PZO 3853
Ursus spelaeus	juvenile	Conturines, Italy	PZO 4142
Ursus spelaeus	juvenile	Conturines, Italy	PZO 4161
Ursus spelaeus	juvenile	Conturines, Italy	PZO 4175
Ursus spelaeus	juvenile	Conturines, Italy	PZO 4199
Ursus spelaeus	juvenile	Conturines, Italy	PZO 5136
Ursus spelaeus	adult	Peștera cu Oase, Romania	CuO 7528-1 (PIUW)
Ursus spelaeus	adult	Peștera cu Oase, Romania	CuO 7528-2 (PIUW)
Ursus spelaeus	adult	Peștera cu Oase, Romania	CuO 7528-3 (PIUW)
Ursus spelaeus	adult	Drachenloch bei Vättis, Switzerland	DR 35 (NMSG)
Ursus spelaeus	adult	Drachenloch bei Vättis, Switzerland	DI.III/IV (NMSG)
Ursus spelaeus	adult	Erpfinger Bärenhöhle, Germany	GPIT.MA.157
Ursus spelaeus	adult	Erpfinger Bärenhöhle, Germany	GPIT.MA.159
Ursus spelaeus	adult	Gamssulzenhöhle, Austria	GS 26-116 (PIUW)
Ursus spelaeus	adult	Gamssulzenhöhle, Austria	GS 129-24 (PIUW)
Ursus spelaeus	juvenile	Gamssulzenhöhle, Austria	GS 51-4 (PIUW)
Ursus spelaeus	adult	Gondenans-les-Moulins, France	NMB Jf.1120 (a)
Ursus spelaeus	adult	Gondenans-les-Moulins, France	NMB Jf.1120 (b)
Ursus spelaeus	adult	Hermannshöhle, Germany	MB.Ma.10881 (MfN)
Ursus spelaeus	adult	Hermannshöhle, Germany	MB.Ma.10886 (MfN)
Ursus spelaeus	juvenile	Hermannshöhle, Germany	MB.Ma.10846 (MfN)
Ursus spelaeus	adult	Križna Jama, Slovenia	VIII-27-3 (NHM)
Ursus spelaeus	adult	Lettenmayerhöhle, Austria	45/1920 (BLZ)
Ursus spelaeus	adult	Lettenmayerhöhle, Austria	45/1920 - 11 (BLZ)
Ursus spelaeus	senile	Loutraki, Greece	LAC 6277b (AUTH)
Ursus spelaeus	juvenile	Loutraki, Greece	LAC 11402 (AUTH)
Ursus spelaeus	adult	Loutraki, Greece	LAC 13046 (AUTH)

Ursus spelaeus	adult	Merkensteinhöhle, Austria	VII-34-3 (NHM)
Ursus spelaeus	adult	Peștera Onceasa, Romania	OnC 7527-1 (PIUW)
Ursus spelaeus	adult	Peștera Onceasa, Romania	OnC 7527-2 (PIUW)
Ursus spelaeus	adult	Peștera Onceasa, Romania	OnC 7527-3 (PIUW)
Ursus spelaeus	adult	Petralona, Greece	PEC 1183 (AUTH)
Ursus spelaeus	adult	Grotta Pocala, Italy	VIII-19-2 (NHM)
Ursus spelaeus	adult	Ramesch Knochenhöhle, Austria	RK 244 (BLZ)
Ursus spelaeus	adult	Ramesch Knochenhöhle, Austria	RK 186 (BLZ)
Ursus spelaeus	adult	Ramesch Knochenhöhle, Austria	RK 425 (BLZ)
Ursus spelaeus	adult	Schwabenreithhöhle, Austria	SW 1596 (PIUW)
Ursus spelaeus	juvenile	Schwabenreithhöhle, Austria	SW 1749 (PIUW)
Ursus spelaeus	juvenile	Schwabenreithhöhle, Austria	SW 1838 (PIUW)
Ursus spelaeus	juvenile	Sloupsko-Šošůvské, Czech Republic	VIII-57-5 (a) (NHM)
Ursus spelaeus	adult	Sloupsko-Šošůvské, Czech Republic	VIII-57-5 (b) (NHM)
Ursus spelaeus	adult	Výpustek, Czech Republic	IX-11-7 (a) (NHM)
Ursus spelaeus	adult	Výpustek, Czech Republic	IX-11-7 (b) (NHM)
Ursus spelaeus	adult	Wildkirchli, Switzerland	WK (NMSG)
Ursus spelaeus	adult	Windener Bärenhöhle, Austria	Wi 56 (PIUW)
Ursus spelaeus	adult	Windener Bärenhöhle, Austria	Wi 59 (PIUW)
Ursus spelaeus	adult	Windener Bärenhöhle, Austria	Wi 65 (PIUW)
Ursus spelaeus	adult	Zoolithenhöhle, Germany	BK 400 (IPUE)
Ursus spelaeus	adult	Zoolithenhöhle, Germany	BK 401 (IPUE)
Ursus spelaeus	adult	Zoolithenhöhle, Germany	BK 402 (IPUE)
Ursus spelaeus	adult	Zoolithenhöhle, Germany	BK 403 (IPUE)
Ursus spelaeus	adult	Zoolithenhöhle, Germany	SCH-1242 (IPUE)
Ursus spelaeus	adult	Zoolithenhöhle, Germany	SCH-1243 (IPUE)
Ursus spelaeus	adult	Zoolithenhöhle, Germany	SCH-1244 (IPUE)
Ursus ursinus	adult	-	MNHN 1879-307

Skeletochronology

Ontogenic changes of bone histology

Femora of neonate cave bears exhibit a fibrolamellar complex with a high amount of woven-fibered bone tissue. In the posterior part of the cortex high amounts of parallel-fibered bone are deposited. The vascularization is mostly longitudinal and reticular and the parallel-fibered bone located posteriorly is less vascularised. With increasing individual age, the amounts of parallel-fibered and lamellar bone within a fibrolamellar complex increases while vascularization changes to predominantly laminar and plexiform arrangement. In the outer cortex of adult animals an avascular OCL is present. In many individuals, a narrow lamellar endosteal layer and/or trabecular bone can be found. A varying amount of parallel-fibered and lamellar bone is the most observed variation in histology among *U. spelaeus* femora (Supplementary Figures 1 & 2). In senile animals a scarcely vascularised mixture of woven-fibered and parallel-fibered bone is present. The few vascular canals are usually longitudinally arranged (Figure 2). Juvenile *U. arctos* exhibit a woven-fibered bone dominated fibrolamellar complex with plexiform and laminar vascularisation. In the innermost part of the cortex, a thin endosteal layer comprised of avascular, laminar bone

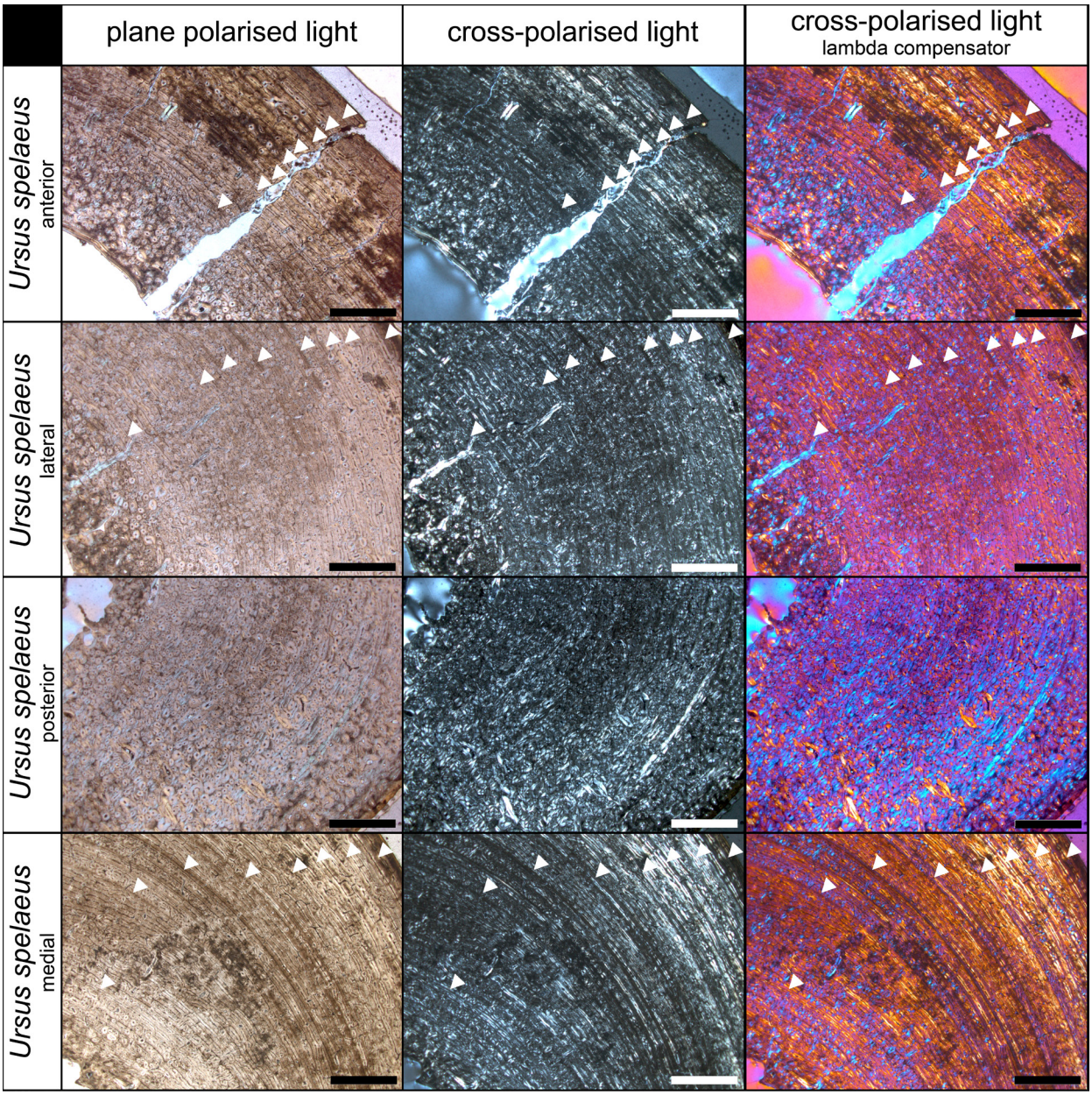

Figure 1. Bone histology of the different parts of the midshaft of cave bear femur MB.Ma.10886 (MfN). White arrow heads indicate LAGs. Note the Haversian bone tissue posteriorly, the distribution of LAGs, and the almost complete resorbtion of the innermost LAG laterally. (Scale bars: 2mm)

can be distinguished. Older animals exhibit a fibrolamellar complex with a higher amount of parallel-fibered bone in the outer parts of the cortex. The vascularisation is laminar and plexiform. The overall change in histology from the inner to the outer part of the cortex is not very distinct. An endosteal layer and OCL are present (Figure 2, Figure 3).

The femora of *U. deningeri* exhibit a fibrolamellar complex with increasing amounts of parallel-fibered bone towards the outer surface of the cortex. The vascularization is primarily laminar and plexiform (Figure 3). *U. americanus* exhibits in the inner part of the cortex a fibrolamellar complex with a high amount of woven-fibered bone and plexiform as well as laminar vascularisation. Towards the outer cortex the amount of parallel-fibered bone increases. A thin, avascular inner and prominent outer circumferential layer can be distinguished

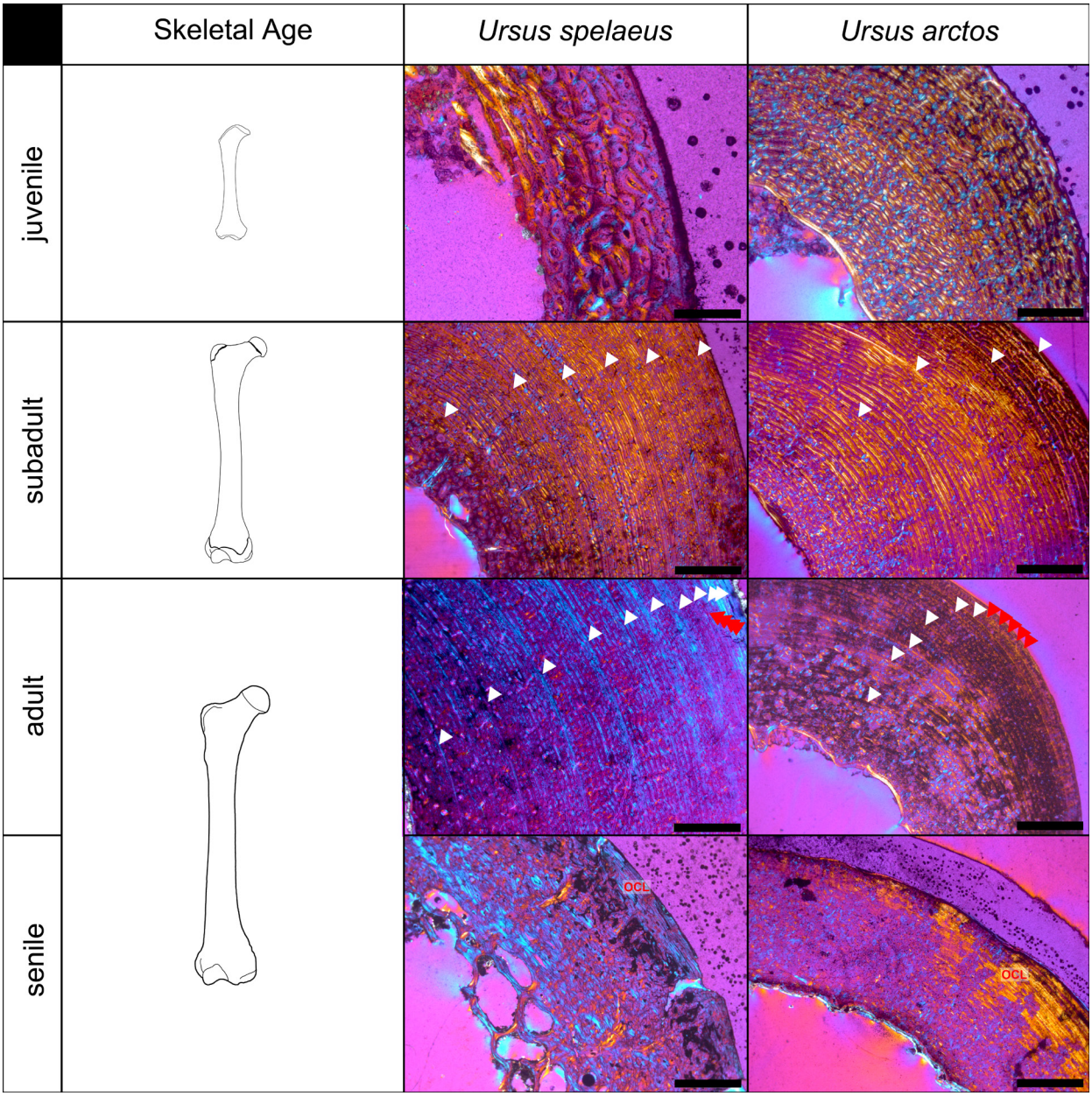

Figure 2: Ontogenetic change of bone histology in the medial part of the femur midshaft of *Ursus spelaeus* and *Ursus arctos* (pictures under cross-polarized light with lambda compensator). White arrow heads indicate LAGs and red arrow heads LAGs of the OCL. Please note that the red arrow heads in the adult *Ursus spelaeus* are flipped. Juvenile *Ursus spelaeus* PZO 5136 (Scale bar: 0.5 mm), subadult *Ursus spelaeus* MB.Ma.10881 (MfN) (Scale bar: 2 mm), adult *Ursus spelaeus* PEC 1183 (AUTH) (Scale bar: 2 mm), senile *Ursus spelaeus* LAC 6277b (AUTH) (Scale bar: 2 mm), juvenile *Ursus arctos* SMNH 2016-5132 (Scale bar: 1 mm), subadult *Ursus arctos* SMNH 2016-5131 (Scale bar: 2 mm), adult *Ursus arctos* SMNH 2016-5025 (Scale bar: 2 mm), senile *Ursus arctos* MNHN 1904-244 (Scale bar: 2 mm).

(Figure 3). Femora of adult *U. maritimus* exhibit a fibrolamellar complex with high amounts of parallel-fibered and lamellar bone as primary tissue. In the outer layer of the cortex a prominent OCL is present (Figure 4). The bone of *U. ursinus* exhibits a very narrow medullary cavity, as also depicted by Mátyás [38]. Overall, histology in *U. ursinus* varies between the anterior, medial, posterior, and lateral portion of the femoral cortex. The anterior part of the bone exhibits a matrix of woven-fibered and parallel-fibered bone with mostly longitudinal and reticular vas-

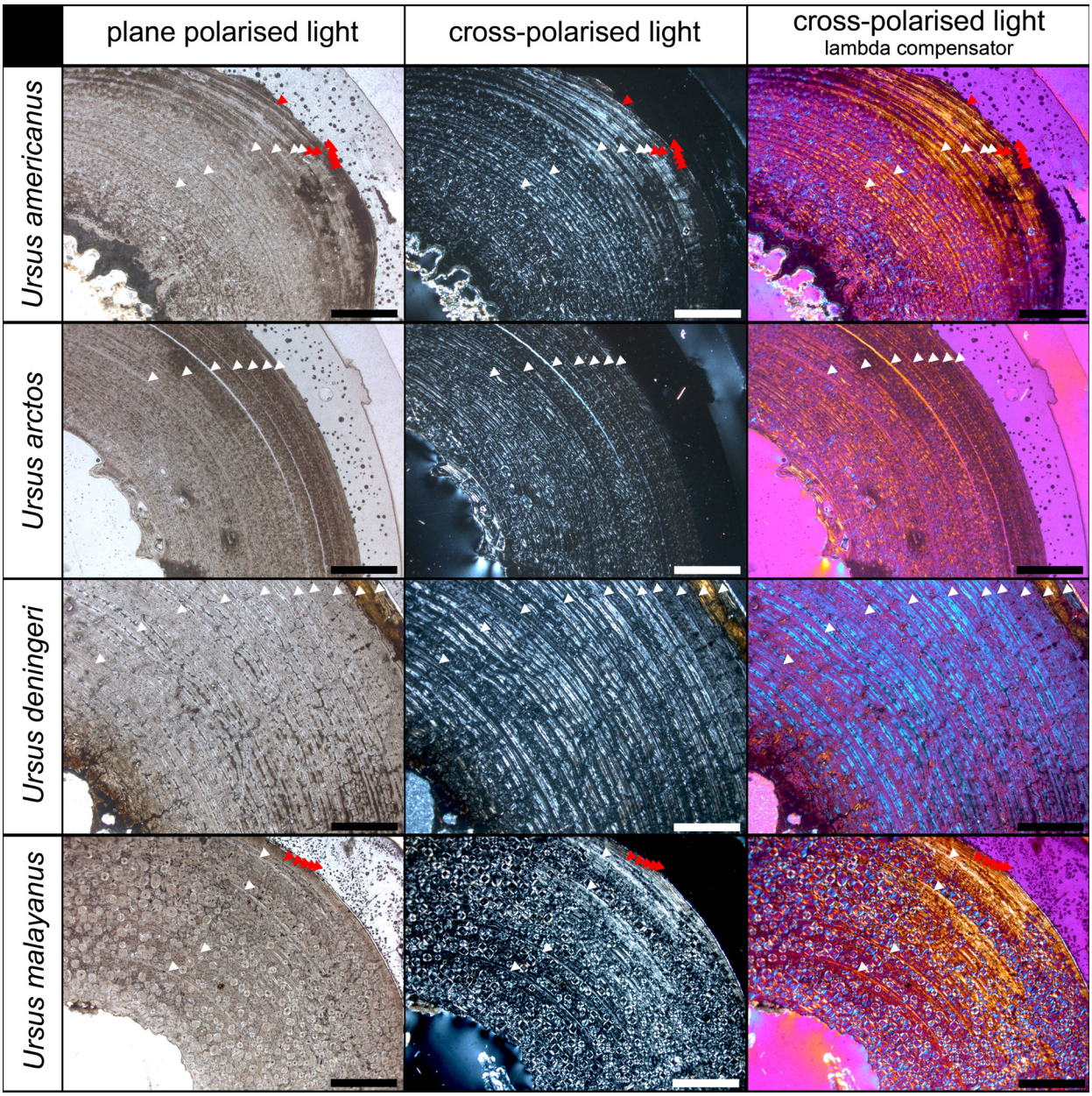

Figure 3: Histology of the medial part of the femur midshaft of *Ursus americanus* (MNHN 1930-208), *Ursus arctos* (MZH KN 1358), *Ursus deningeri* (HJ 151), and *Ursus malayanus* (MNHN 1914-360). White arrow heads indicate LAGs and red arrow heads LAGs of the OCL. (Scale bars: 2 mm)

cularization in the inner part of the cortex. The outer part of the cortex of the anterior face of the bone shows an increase in parallel-fibered bone and a distinct avascular OCL. Medially, the inner cortex of the bone is comprised of woven-fibered bone with mostly longitudinal and reticular vascularization whereas the outer cortex exhibits parallel-fibered bone with low amounts of laminar vascularization and layers of avascular lamellar bone. Medially, the lamellar bone of the OCL is interlayered several times by woven-fibered bone with longitudinal and reticular vascularization (Figure 4). The lateral and posterior parts of the thin section exhibit little primary bone tissue. Laterally, the outer cortex exhibits avascular lamellar bone interrupted by woven-fibered bone with laminar and reticular vascularization.

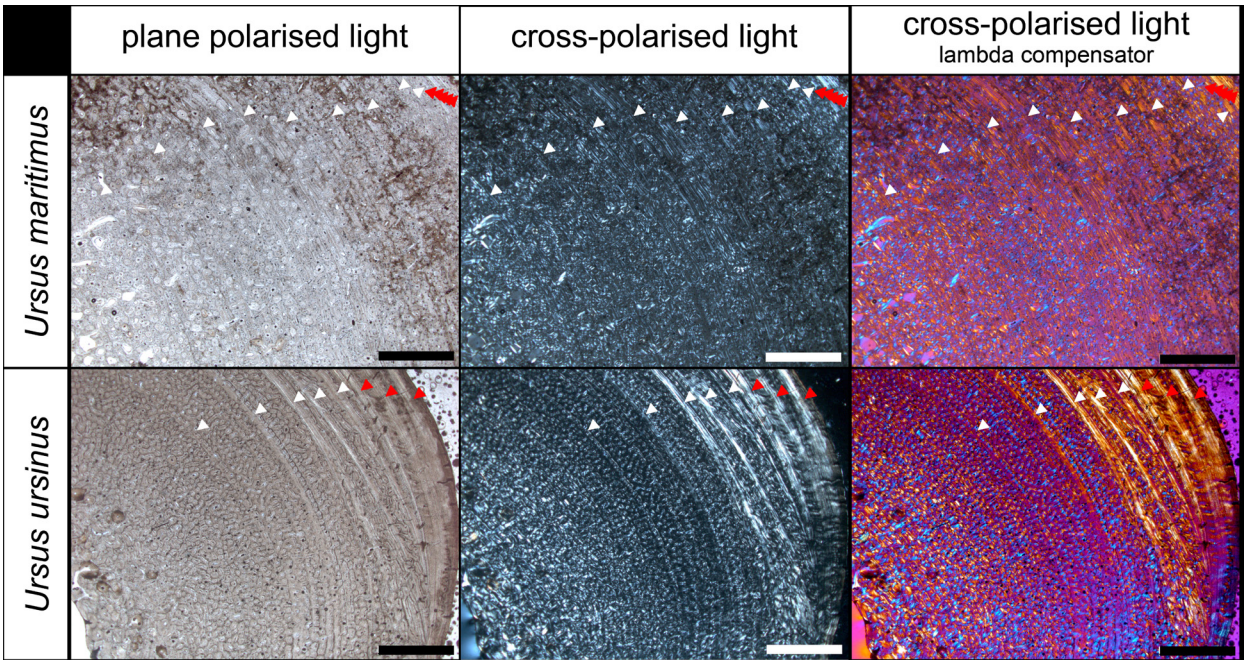

Figure 4: Histology of the medial part of the femur midshaft of *Ursus maritimus* (MZH UN 2355) and *Ursus ursinus* (MNHN 1879-307). White arrow heads indicate LAGs and red arrow heads LAGs of the OCL. Please note that the last white arrow head and the red arrow heads of the OCL are flipped in *Ursus maritimus*. (Scale bars: 2 mm)

The femur of *U. malayanus* exhibits little primary bone tissue. In the anterior and lateral part of the bone the central cortex exhibits a fibrolamellar complex. The outer part of the cortex shows an increase in parallel-fibered bone with a distinct OCL. Medially, the cortex exhibits a fibrolamellar complex with laminar and plexiform vascularization. Towards the OCL, the deposition of parallel-fibered bone increases (Figure 3).

Secondary Bone

Bone remodelling in *U. spelaeus* starts in the posterior inner cortex with scattered secondary osteons. In the inner part of the cortex, especially posteriorly, dense Haversian bone is present already in young individuals. In older individuals, scattered secondary osteons are found in many parts of the cortex, but secondary remodelling is especially prevalent anteriorly. Posteriorly, around the linea aspera, the dense Haversian bone reaches the outer surface of the cortex (Figure 1, Figure 2). In their first year, the femora of *U. arctos* exhibit no secondary remodelling of the bone. First signs of remodelling start in the posterior part of the bone around the linea aspera. Over time, a dense Haversian bone tissue forms with several generations of secondary osteons, which reach the outer surface of the cortex. In the other regions of the bone, secondary remodelling starts in the inner part of the cortex with scattered secondary osteons. With increasing age more scattered secondary osteons appear also in outer parts of the cortex. In old animals, a dense Haversian bone tissue forms in the inner cortex of the bone (Figure 2). In *U. deningeri* bone remodelling is most pronounced around the linea aspera in the posterior part of the bone. Here, Haver-

sian bone is dense and reaches the outer part of the cortex. In other parts of the bone few scattered secondary osteons are present, especially in the inner part of the cortex. In *U. americanus* secondary remodelling starts in the inner part of the cortex and can lead to a layer of Haversian bone tissue in the innermost part of the cortex. Around the area of the linea aspera, Haversian bone tissue with overlapping generations of secondary osteons is found and can even reach the outer surface of the cortex. Secondary osteons are found scattered over the whole cortex in all parts of the bone but are more abundant in the anterior and lateral part of the bone. The femora of skeletally mature *U. maritimus* exhibit dense Haversian bone with several successive generations of secondary osteons in the inner part of the cortex. In the area of the linea aspera, the secondary tissue extends until the outer surface of the cortex. In other parts of the bone many scattered secondary osteons are present in the outer part of the cortex. Besides the area around the linea aspera, the anterior part exhibits the highest bone remodelling. Bone remodelling in *U. ursinus* is uneven. Comparable to all other bear species the posterior part of the thin section, at the linea aspera, exhibits a dense Haversian bone tissue with several successive generations of secondary osteons. Medially, secondary osteons are rare and mostly found in the innermost part of the cortex. In the anterior region more secondary osteons are present and in the inner part of the cortex Haversian bone tissue is present, which is increasingly pronounced towards the lateral part of the bone. The thin section of *U. malayanus* exhibits dense Haversian bone tissue with several overlapping generations of secondary osteons in the innermost part of the cortex. Posteriorly, this Haversian bone tissue extends to the outer cortex. In the anterior and lateral part of the thin sections many secondary osteons, partly overlapping, are scattered over the whole cortex except in the outermost part. The medial region of the bone shows the least amount of secondary remodelling but a considerable amount of secondary osteons is still present.

Growth marks and growth in cave bears and related species

All examined bear species and cave bear populations with preserved histology exhibit LAGs. In cave bears, the first LAG is resorbed around the time the 6th is built (Figure 2). The ontogenetic series of *U. arctos* shows that the amount of LAGs is consistently below the minimum age documented for the individual evidencing the loss of one LAG as well. The loss of the first LAG and the first growth zone was therefore inferred for all bear species within the study. Growth zones of cave bears commonly exhibit a peculiar regular pattern. After the termination by a previous LAG, the growth zone starts with the deposition of woven-fibered bone. Over time, the amount of parallel-fibered bone increases and finally the growth zone terminates in a LAG. This pattern can be obscured due to the overall increase of parallel-fibered and lamellar bone. In contrast, in *U. arctos*, *U. americanus*, and *U. ursinus*, the growth zone is mostly a

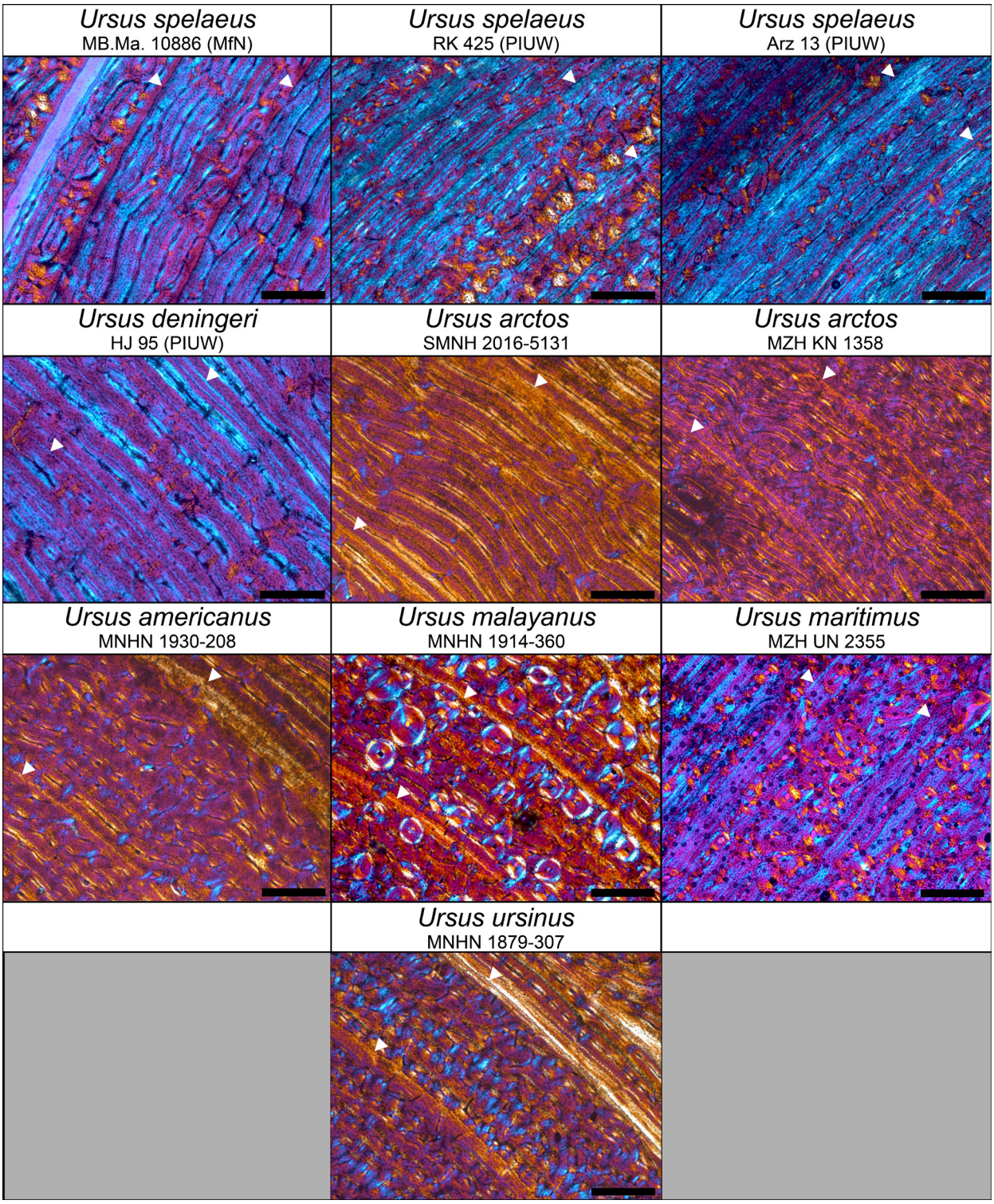

Figure 5: Comparison of the growth zones among different bear species (pictures under cross-polarized light with lambda compensator). White arrow heads indicate LAGs. (Scale bars: 0.5 mm)

layer of a uniform fibrolamellar complex and only close to the cessation of growth, marked by a LAG, a thin layer of parallel-fibered bone is produced. The growth zones of *U. deningeri*, *U. malayanus*, and *U. ursinus* are less uniform and exhibit somewhat alternating parallel-fibered and woven-fibered bone in the fibrolamellar complex (Figure 5).

The timing of the cessation of overall circumferential bone growth is indicated by the OCL [27]. Usually, an OCL is a layer

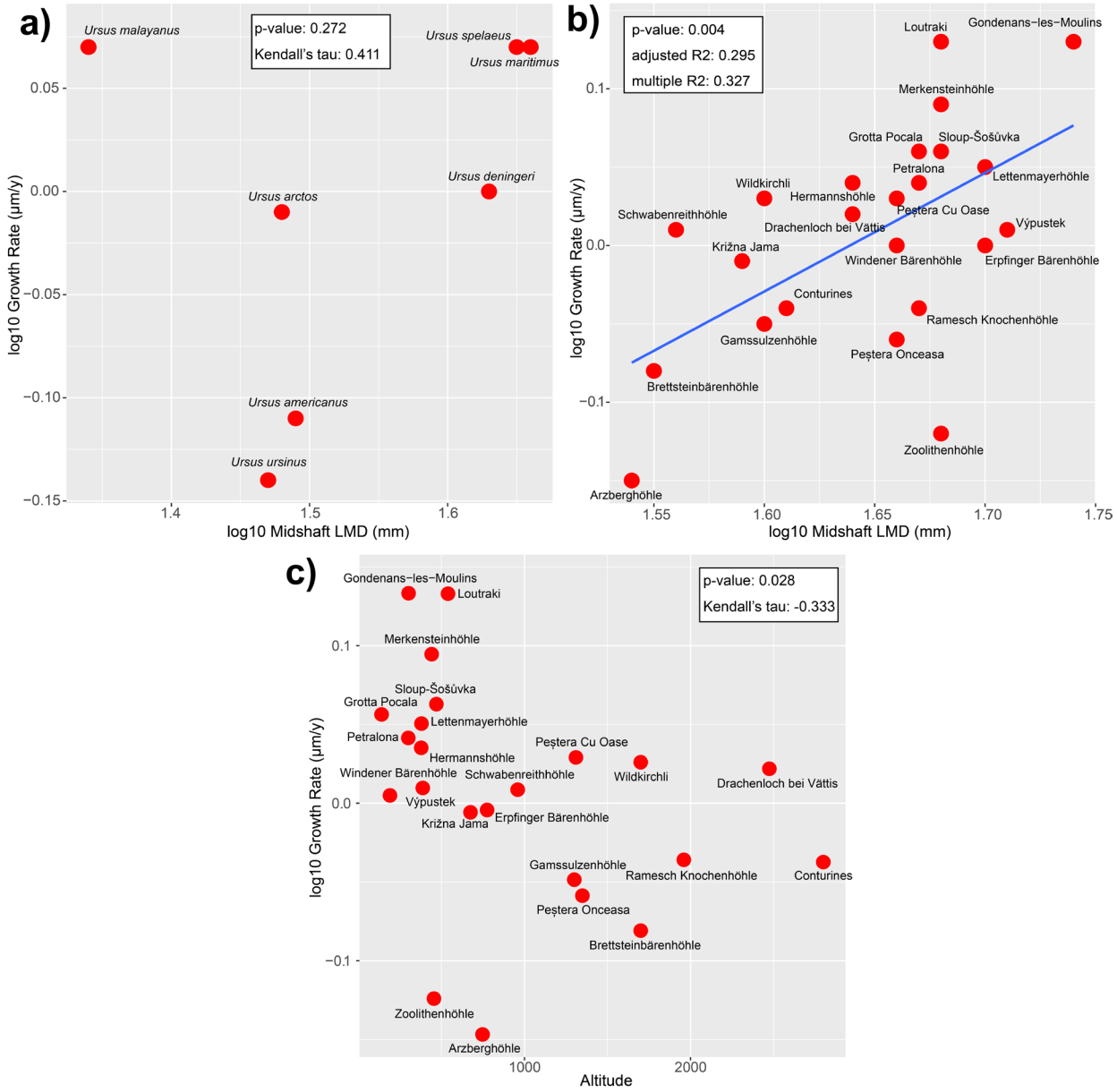

Figure 6: a) Kendall's tau correlation of growth rate of different bear species compared to their latero-medial diameter as a proxy for body size. b) Linear model of growth rate of different cave bear localities compared to their latero-medial diameter as a proxy for body size. c) Kendall's tau correlation of growth rate of different cave bear localities compared to the altitude of the locality.

of avascular lamellar bone with potentially closely spaced LAGs. The OCL of cave bears appears between LAG 10 – 13 and in *U. arctos* it appears between LAG 6 - 7. Skeletal maturity was reached in *U. americanus* after LAG 7, in *U. malayanus* after LAG 5, in *U. maritimus* after LAG 10, and in *U. ursinus* after LAG 6. No OCL was recorded in *U. deningeri*, suggesting that this animal did not reach skeletal maturity before the age of 11 (10 LAGs plus resorbed, Figure 3).

The overall growth speed is not correlated with latero-medial length as proxy for size. The fastest growing species were *U. malayanus*, *U. maritimus*, and *U. spe-*

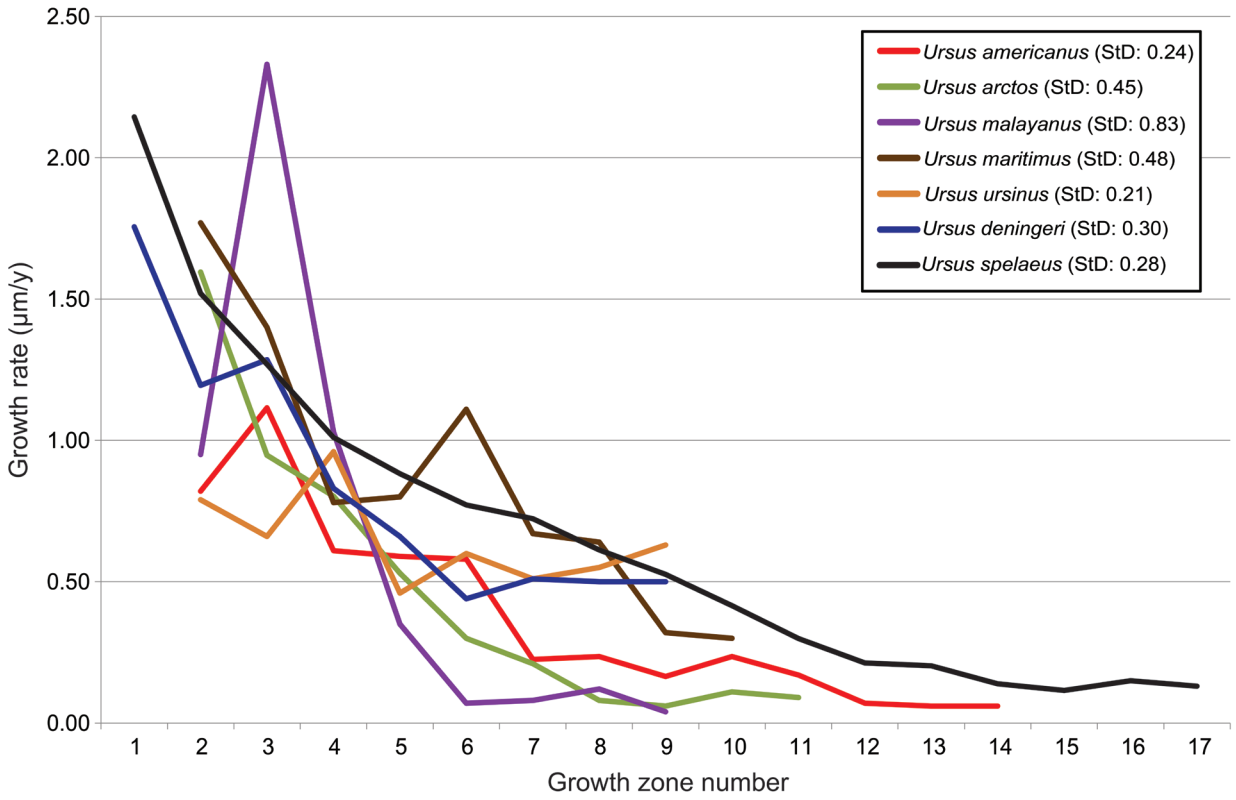

Figure 7: Mean growth rates among different bear species. Evenness of growth is expressed as standard deviation (StD) from growth zone two to five.

laeus, the slowest growing species were *U. americanus* and *U. ursinus* (Figure 6a). Looking at a standardized growth period among different cave bear localities, there is a considerable amount of variation in the speed of growth. Within cave bears, growth was significantly correlated with size. The slowest growth was recorded for Arzberghöhle, Zoolithenhöhle, and Brettsteinbärenhöhle whereas the fastest growth was documented for Loutraki and Gondenans-les-Moulin (Figure 6b). Despite the high degree of variation, the speed of growth correlates with the altitude of the locality, albeit not linearly (Figure 6c).

Among different bear species the most even growth patterns were documented in *U. ursinus* and *U. americanus* and the most uneven one in *U. malayanus* (Figure 7). The most even growth was recorded for Erpfinger Bärenhöhle, Ramesch Knochenhöhlen, and Zoolithenhöhle. Growth was most uneven in the samples from Schwabenreithhöhle, Merkensteinhöhle, and Drachenloch bei Vättis (Figure 8). The evenness of growth is not correlated with altitude (Kendall's tau: 0.095, p-value: 0.553).

Discussion

The presence of a fibrolamellar complex in bear species follows previously described thin sections [39]. However, notable differences were encountered in the composition of the fibrolamellar complex. Whereas, *U. spelaeus*, *U. arctos*, and *U. americanus* exhibit a bone histological pattern similar to the one described by Enlow and Brown [39], the one in other

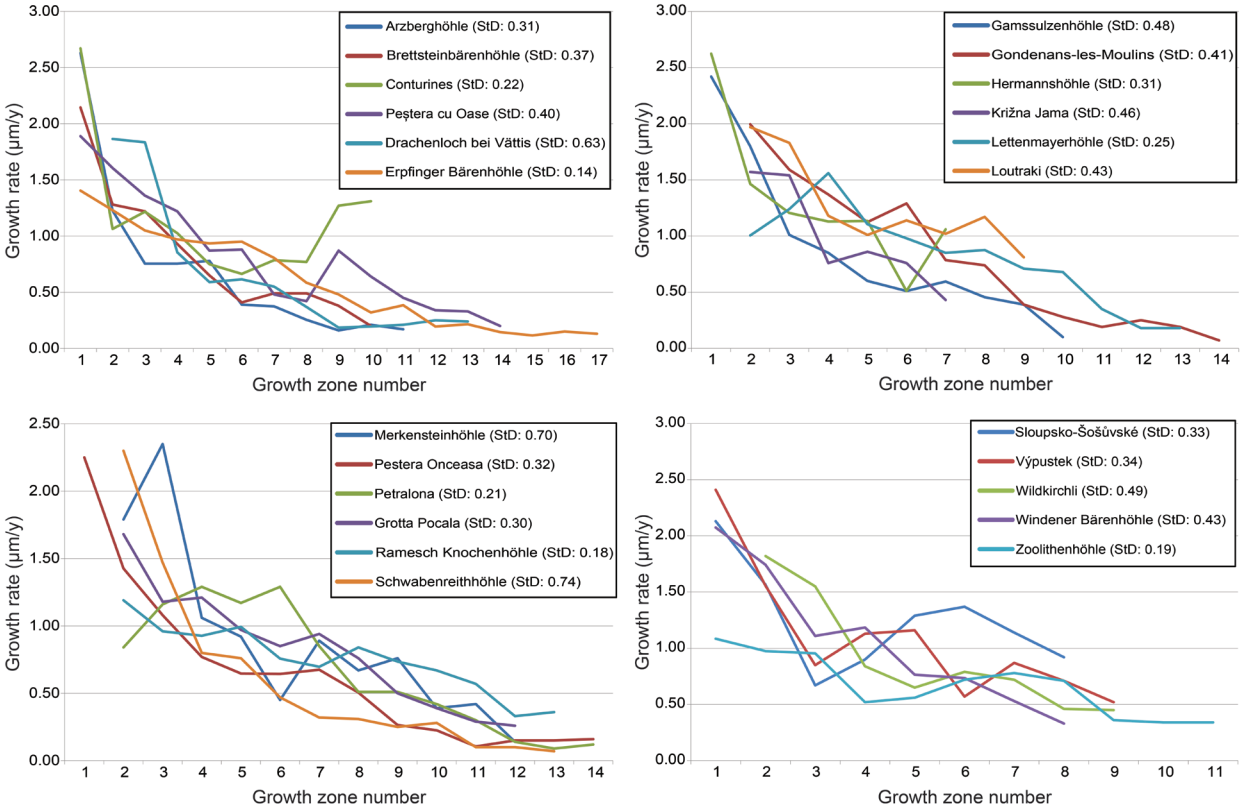

Figure 8: Mean growth rates among different cave bear localities. Evenness of growth is expressed as standard deviation (StD) from growth zone two to seven.

bear species is characterized by higher amounts of parallel-fibered and lamellar bone. A notable difference was found in *U. ursinus* with considerable amounts of longitudinal vascular canals only present in this species. One of the first histological examinations of *U. spelaeus* from the Drachenhöhle of Mixnitz described lamellar bone structure within trabecular bone [40]. If present, the trabecular bone of the examined species consisted of lamellar bone, which is commonly found [27]. Later studies on cave bear histology focused on mineralogical examinations of remains to investigate taphonomic processes [41] or pathological changes to bone substance [42]. The ontogenetic change of bone tissue in *U. arctos* and *U. spelaeus* mirrors findings in deer femora with the exception that remodelling in bears starts in the inner cortex [19]. A common bias when analysing histology from transversal thin section is the overestimation of the amount of woven-fibered bone in a fibrolamellar complex [28]. The potential for this bias was verified in cave bear femora (Figure 9). The longitudinal section indicates that there is actually only a small amount of woven-fibered bone in the fibrolamellar complex, less than would be expected from the transverse section. Part of what looks like woven-fibered bone is likely parallel-fibered bone with longitudinal crystallite orientation [28]. The cessation of bone growth as marked by an OCL has been associated with either sexual maturity [43, 44] or skeletal maturity [19]. In *U. arctos*, femora reach skeletal maturity between 5 - 8 years [45] and animals reach sexual maturity be-

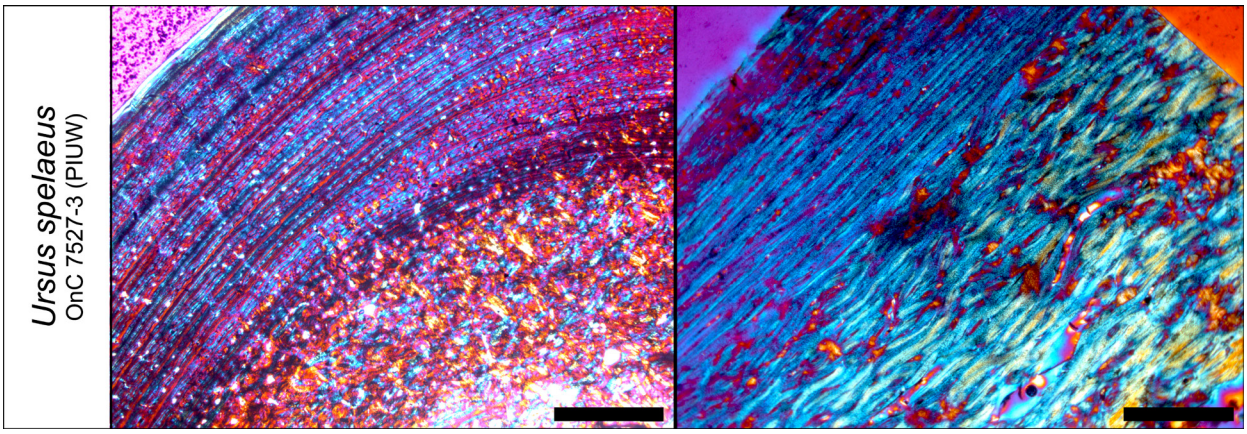

Figure 9: Picture of the femoral cortex of *Ursus spelaeus* from Peștera Onceasa, Romania under cross-polarized light with lambda compensator. Transverse thin section (left) exhibits more woven-fibered bone than longitudinal section (right). (Scale bar: 2 mm)

tween the age of 3.5 - 5.5 years [46]. The OCL in *U. arctos* is produced between 7 – 8 years (6 – 7 LAGs plus one resorbed) suggesting that, at least in bears, the OCL indeed indicates skeletal maturity. For the other examined bear species the age of skeletal maturity for femora is not known but the appearance of the OCL cannot be linked to sexual maturity [46]. In cave bears, the OCL appears between LAG 10 and 13, which suggest a high age of attaining femoral skeletal maturity.

The secondary remodelling of the femora of all examined bear species generally follows a very similar spatial pattern. Haversian tissue is dense around the linea aspera and the inner part of the cortex whereas in the rest of the bone more scattered secondary osteons are present. A similar pattern of secondary remodelling was described by Mátyás [38]. In deer, secondary remodelling is also strongest close to the linea aspera [19]. The amount of scattered secondary osteons among the different examined bear species does vary considerably. Non-hibernating bears such as *U. malayanus* and *U. maritimus* (Figure 3, Figure 4) [46] exhibit many scattered secondary osteons in their bone cortex. In contrast, bears which exhibit hibernating behaviour such as *U. arctos*, *U. americanus*, and *U. spelaeus* [46] have fewer remodelling throughout the cortex. Hibernation does influence the speed of bone deposition and resorption in bears [17], which might be the cause for the observed differences in bone remodelling.

Cave bears grew at high rates. This is in contrast to some predictions based on histological observations. The histology of *U. americanus* and *U. arctos* suggests a faster growth speed than is recorded because of the larger amounts of woven-fibered bone. On the other hand, *U. maritimus* exhibits a great amount of slowly deposited parallel-fibered and lamellar bone. However, in contrast to artiodactyls [20], growth periods during the year are not known for bear species. As aforementioned, bears slow down bone deposition and resorption during hibernation [17]. Thus the extent of the cessation of growth between species could be different. Another factor to consider is that the length of hibernation varies among populations of

one species [46]. The observed variation in growth speed among cave bears from different localities was best explained by the altitude of the cave. High alpine cave bear populations are smaller than their lowland counterparts [13] and grow at a slower pace. However, the change is not gradual. Above an altitude of about 500 m, the pace of growth slows down considerably. In contrast, the latero-medial length of the femora midshaft is linearly correlated with altitude (Supplementary Figure 3).

Growth speed of *U. spelaeus* and *U. maritimus* are very similar. However, the biology of both animals is very different with one being a denning carnivore [46] and the other a hibernating herbivore [3]. Cave bear pups had about the same size as the ones of *U. arctos* at birth [47, 48] and thus grew faster and longer to attain their adult stature of 500 kg [49] or possibly even up to 1500 kg [3]. The maximum known age for cave bears is 30 years [50]. However, most individuals did not reach that age as mortality was often high among juveniles [50-52]. The fast pace of growth in cave bears suggest an early age of maturation [53]. Despite this not being the case for skeletal maturity, sexual maturity could have been attained early in life of cave bears, which could have compensated for high juvenile mortality. Based on life history theory, a high juvenile mortality rate would favour early sexual maturity, large litter sizes, and rapid growth [54, 55]. A small birth weight and big litter size for cave bears would be in concordance with carnivoran life history strategy [56]. Nonetheless, the size [3, 49] and longevity [52] of cave bears exhibit the complex nature of species specific life history strategies.

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References

1. Barnosky AD, Koch PL, Feranec RS, Wing SL, Shabel AB (2004). Assessing the causes of Late Pleistocene extinctions on the continents. Science. 306(5693):70-5.
2. Lorenzen ED, Nogues-Bravo D, Orlando L, Weinstock J, Binladen J, Marske KA, Ugan A, Borregaard MK, Gilbert MP, Nielsen R, Ho SYW, Goebel T, Graf KE, Byers D, Stenderup JT, Rasmussen M, Campos PF, Leonard JA, Koepfli K-P, Froese D, Zazula G, Stafford TW, Aaris-Sorensen K, Batra P, Haywood AM, Singarayer JS, Valdes PJ, Boeskorov G,

Burns JA, Davydov SP, Haile J, Jenkins DL, Kosintsev P, Kuznetsova T, Lai X, Martin LD, McDonald HG, Mol D, Meldgaard M, Munch K, Stephan E, Sablin M, Sommer RS, Sipko T, Scott E, Suchard MA, Tikhonov A, Willerslev R, Wayne RK, Cooper A, Hofreiter M, Sher A, Shapiro B, Rahbek C, Willerslev E (2011). Species-specific responses of Late Quaternary megafauna to climate and humans. Nature. 479(7373):359-64.

3. Rabeder G, Nagel D, Pacher M (2000). Der Höhlenbär. Stuttgart: Thorbecke Verlag.
4. Knapp M, Rohland N, Weinstock J, Baryshnikov G, Sher A, Nagel D, Rabeder G, Pinhasi R, Schmidt HA, Hofreiter M (2009). First DNA sequences from Asian cave bear fossils reveal deep divergences and complex phylogeographic patterns. Mol Ecol. 18(6):1225-38.
5. Bon C, Caudy N, de Dieuleveult M, Fosse P, Philippe M, Maksud F, Beraud-Colomb É, Bouzaid E, Kefi R, Laugier C, Rousseau B, Casane D, van der Pflicht J, Elalouf J-M (2008). Deciphering the complete mitochondrial genome and phylogeny of the extinct cave bear in the Paleolithic painted cave of Chauvet. PNAS. 105(45):17447-52.
6. Krause J, Unger T, Noçon A, Malaspinas A-S, Kolokotronis S-O, Stiller M, Soibelzon L, Spriggs H, Dear PH, Briggs AW, Bray SCE, O'Brien SJ, Rabeder G, Matheus P, Cooper A, Slatkin M, Pääbo S, Hofreiter M (2008). Mitochondrial genomes reveal an explosive radiation of extinct and extant bears near the Miocene-Pliocene boundary. BMC Evol Biol. 8(1):1-12.
7. Bocherens H (2015). Isotopic tracking of large carnivore palaeoecology in the mammoth steppe. Quat Sci Rev. 117:42-71.
8. Rabeder G, Hofreiter M (2004). Der neue Stammbaum der alpinen Höhlenbären. Die Höhle. 55:58-77.
9. Bocherens H, Fizet M, Mariotti A (1994). Diet, physiology and ecology of fossil mammals as inferred from stable carbon and nitrogen isotope biogeochemistry: implications for Pleistocene bears. Palaeogeogr Palaeoclimatol Palaeoecol. 107(3):213-25.
10. Dabney J, Knapp M, Glocke I, Gansauge M-T, Weihmann A, Nickel B, Valdiosera C, García N, Pääbo S, Arsuaga J-L, Meyer M (2013). Complete mitochondrial genome sequence of a Middle Pleistocene cave bear reconstructed from ultrashort DNA fragments. PNAS. 110(39):15758-63.
11. Stiller M, Molak M, Prost S, Rabeder G, Baryshnikov G, Rosendahl W, Münzel S, Bocherens H, Grandal-d'Anglade A, Hilpert B, Germonpré M, Stasyk O, Pinhasi R, Tintori A, Rohland N, Mohandesan E, Ho SYW, Hofreiter M, Knapp M (2014). Mitochondrial DNA diversity and evolution of the Pleistocene cave bear complex. Quat Int. 339-340:224-31.
12. Baca M, Mackiewicz P, Stankovic A, Popović D, Stefaniak K, Czarnogórska K, Nadachowski A, Gąsiorowski M, Hercman H, Weglenski P (2014). Ancient DNA and dating of cave bear remains from Niedźwiedzia Cave suggest early appearance of *Ursus ingressus* in Sudetes. Quat Int. 339-340:217-23.
13. Rabeder G, Hofreiter M, Nagel D, Withalm G (2004). New taxa of Alpine cave bears (Ursidae, Carnivora). Cah Sci. Hors série 2:49-67.
14. Fortes GG, Grandal-d'Anglade A, Kolbe B, Fernandes D, Meleg IN, García-Vázquez A, Pinto-Llona AC, Constantin S, de Torres TJ, Ortiz JE, Frischauf C, Rabeder G, Hofreiter M, Barlow A (2016). Ancient DNA reveals differences in behaviour and sociality between brown bears and extinct cave bears. Mol Ecol. 25(19):4907-18.
15. Giangregorio L, Blimkie CJR (2002). Skeletal adaptations to alterations in weight-

bearing activity. Sports Med. 32(7):459-76.

16. McGee-Lawrence M, Buckendahl P, Carpenter C, Henriksen K, Vaughan M, Donahue S (2015). Suppressed bone remodeling in black bears conserves energy and bone mass during hibernation. J Exp Biol. 218(13):2067-74.
17. McGee-Lawrence ME, Carey HV, Donahue SW (2008). Mammalian hibernation as a model of disuse osteoporosis: the effects of physical inactivity on bone metabolism, structure, and strength. Am J Physiol Regul Integr Comp Physiol. 295(6):R1999-R2014.
18. Nacarino-Meneses C, Jordana X, Köhler M (2016). First approach to bone histology and skeletochronology of *Equus hemionus*. C R Palevol. 15(1–2):267-77.
19. Kolb C, Scheyer TM, Lister AM, Azorit C, de Vos J, Schlingemann MA, Rössner GE, Monaghan NT, Sánchez-Villagra MR (2015). Growth in fossil and extant deer and implications for body size and life history evolution. BMC Evol Biol. 15(1):19.
20. Köhler M, Marín-Moratalla N, Jordana X, Aanes R (2012). Seasonal bone growth and physiology in endotherms shed light on dinosaur physiology. Nature. 487:358–61.
21. Köhler M, Moyà-Solà S (2009). Physiological and life history strategies of a fossil large mammal in a resource-limited environment. PNAS. 106(48):20354-8.
22. Amson E, Kolb C, Scheyer TM, Sánchez-Villagra MR (2015). Growth and life history of Middle Miocene deer (Mammalia, Cervidae) based on bone histology. C R Palevol. 14(8):637-45.
23. Kolb C, Scheyer TM, Veitschegger K, Forasiepi AM, Amson E, Van der Geer AAE, Van den Hoek Ostende L, Hayashi S, Sánchez-Villagra MR (2015). Mammalian bone palaeohistology: a survey and new data with emphasis on island forms. PeerJ. 3:e1358.
24. Castanet J, Francillon-Vieillot H, Meunier FJ, de Ricqlès A (1993). Bone and individual aging. In: Hall BK, editors. Bone Volume 7: Bone growth - B. Boca Raton: CRC Press. p. 245-83.
25. Amprino R (1947). La structure du tissu osseux envisagee comme expression de differences dans la vitesse de l'accroissement. Archives de Biologie. 58:315-30.
26. de Margerie E, Robin JP, Verrier D, Cubo J, Groscolas R, Castanet J (2004). Assessing a relationship between bone microstructure and growth rate: a fluorescent labelling study in the king penguin chick (*Aptenodytes patagonicus*). J Exp Biol. 207(5):869.
27. Huttenlocker AK, Woodward HN, Hall BK (2013). The biology of bone. In: Padian K, Lamm E-T, editors. Bone histology of fossil tetrapods - advancing methods, analysis, and interpretation. Berkeley and Los Angeles: University of California Press. p. 13-34.
28. Stein K, Prondvai E (2014). Rethinking the nature of fibrolamellar bone: an integrative biological revision of sauropod plexiform bone formation. Biol Rev. 89(1):24-47.
29. Hinrichs J (2016). Are lines of arrested growth in bone indicative of seasonal metabolic supression in bears. Fort Collins, Colorado: Colorado State University.
30. Marangoni F, Schaefer E, Cajade R, Tejedo M (2009). Growth-mark formation and chronology of two neotropical anuran species. J Herpetol. 43(3):546-50.
31. Buffrénil V, Castanet J (2000). Age Estimation by Skeletochronology in the Nile Monitor (*Varanus niloticus*), a highly exploited species. J Herpetol. 34(3):414-24.
32. Castanet J, Croci S, Aujard F, Perret M, Cubo J, Margerie E (2004). Lines of arrested growth in bone and age estimation in a small primate: *Microcebus murinus*. J Zool. 263:31-39.
33. Chinsamy A, Raath MA (1992). Preparation of fossil bone for histological exami-

nation. Palaeontol afr. 29:39-44.

34. Sander PM, Andrassy P (2006). Lines of arrested growth and long bone histology in Pleistocene large mammals from Germany: what do they tell us about dinosaur physiology? Palaeontogr Abt A. 277:143-59.
35. R Development Core Team (2015). R: A language and environment for statistical computing. Version 3.2.3. http://www.R-project.org
36. Wickham H (2009). ggplot2: Elegant graphics for data analysis. New York: Springer-Verlag.
37. McLeod AI (2011). Kendall: Kendall rank correlation and Mann-Kendall trend test. R package version 2.2. https://CRAN.R-project.org/package=Kendall
38. Mátyás J (1955). Mikroskopische Untersuchungen der biologischen Resorptionen in den Röhrenknochen. Budapest: Akadémiai Kiadó.
39. Enlow DH, Brown SO (1958). A comparative histological study of fossil and recent bone tissues. Part III. Tex J Sci. 10:187-230
40. Breuer R (1931). Zur Anatomie, Pathologie und Histologie der Zähne und der Kiefer von Ursus spelaeus. In: Abel O, Kyrle G, editors. Die Drachenhöhle bei Mixnitz. Speläologische Monographien 7/8. Wien: Österreichische Staatsdruckerei. p. 581-623.
41. Rogóż A, Sawłowicz Z, Socha P, Stefaniak K (2009). Mineralization of teeth and bones of the cave bear (*Ursus spelaeus*) from the Biśnik Cave, Southern Poland. Mineralogia. 40(1-4):65–84.
42. Nowakowski D, Stefaniak K (2015). Pathological changes of the cranium of a young female cave bear (*Ursus spelaeus* R.)-a case study (the Sudety Mts, Poland). Int J Osteoarchaeol. 25(1):119-25.
43. Jordana X, Marín-Moratalla N, Moncunill-Solè B, Nacarino-Meneses C, Köhler M (2016). Ontogenetic changes in the histological features of zonal bone tissue of ruminants: a quantitative approach. C R Palevol. 15(1–2):255-66.
44. Marin-Moratalla N, Jordana X, Köhler M (2013). Bone histology as an approach to providing data on certain key life history traits in mammals: implications for conservation biology. Mamm Biol. 78: 422–429.
45. Weinstock J (2009). Epiphyseal fusion in brown bears: a population study of grizzlies (*Ursus arctos horribilis*) from Montana and Wyoming. Int J Osteoarchaeol. 19(3):416-23.
46. Hunter L (2011). Carnivores of the world. Princeton (New Jersey): Princeton University Press.
47. Ehrenberg K (1931). Die Variabilität der Backenzähne beim Höhlenbären. In: Abel O, Kyrle G, editors. Die Drachenhöhle bei Mixnitz. Speläologische Monographien 7/8. Wien: Österreichische Staatsdruckerei. p. 537-73.
48. Ehrenberg K (1973). Ein fast vollständiges Höhlenbärenneonatenskelett aus der Salzofenhöhle im Toten Gebirge. Ann Nathist Mus Wien. 77:69-113.
49. Christiansen P (1999). What size were *Arctodus simus* and *Ursus spelaeus* (Carnivora: Ursidae)? Ann Zool Fenn. 36(2):93-102.
50. Debeljak I (2007). Fossil population structure and mortality of the cave bear from the Mokrica cave (North Slovenia). Acta Carsologica. 36(3):475-84.
51. Grandal-D'Anglade A, Vidal Romaní JR (1997). A population study on the cave bear (*Ursus spelaeus* Ros.-Hein.)) from Cova Eirós (Triacastela, Galicia, Spain). Geobios. 30(5):723-31.
52. Debeljak I (2011). Determination of individual age and season at death in cave bear from Ajdovska jama near Krško (Slovenia). In: Pacher M, Pohar V, Rabeder G, editors. Ajdovska Jama - Palaeontology, zoology and archaeology of Ajdovska Jama near Krško in Slovenia. Mitteilungen der Kommission für Quartär-

forschung der östereichischen Akademie der Wissenschaften, Volume 20. Wien: Österreichische Akademie der Wissenschaften. p. 51-63.

53. Stearns SC (2000). Life history evolution: successes, limitations, and prospects. Naturwissenschaften. 87(11):476-86.

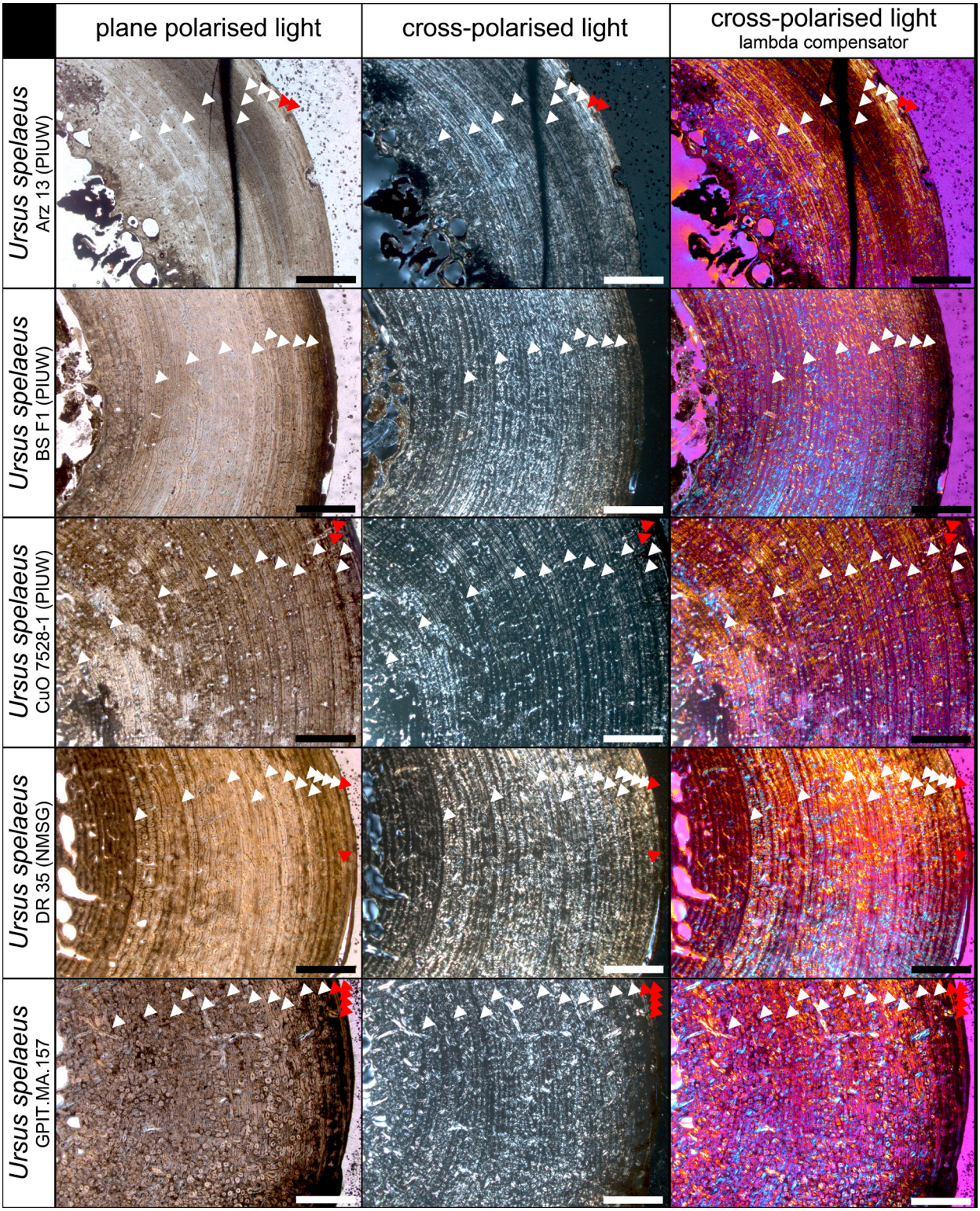
54. Charnov EL (1993). Life history invariants: some explorations of symmetry in evolutionary ecology. Oxford: Oxford University Press.

55. Charnov EL (1991). Evolution of life history variation among female mammals. PNAS. 88(4):1134-7.

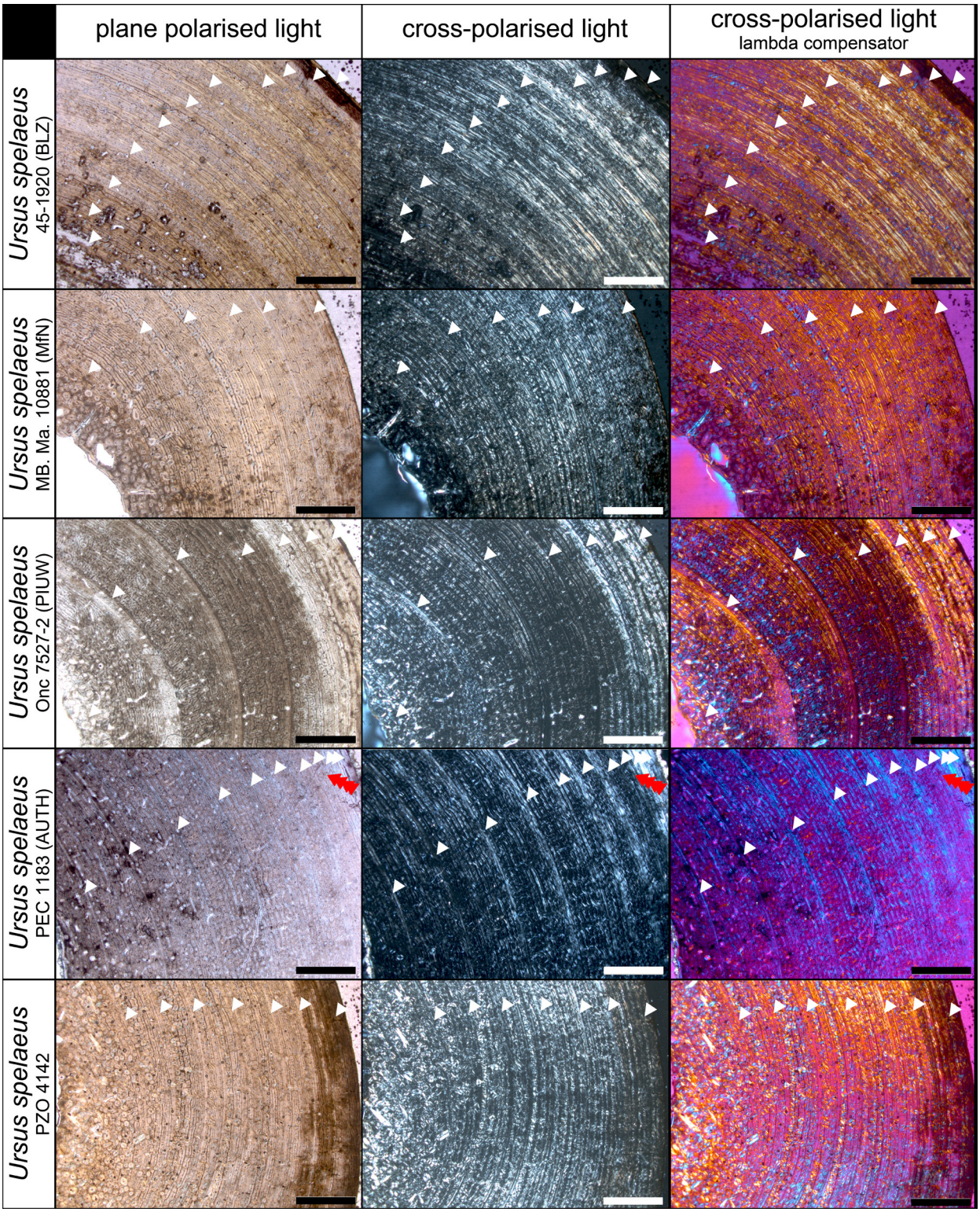
56. Sibly RM, Brown JH (2009). Mammal reproductive strategies driven by offspring mortality-size relationships. Am Nat. 173(6):E185-E99.

Supplementary Information

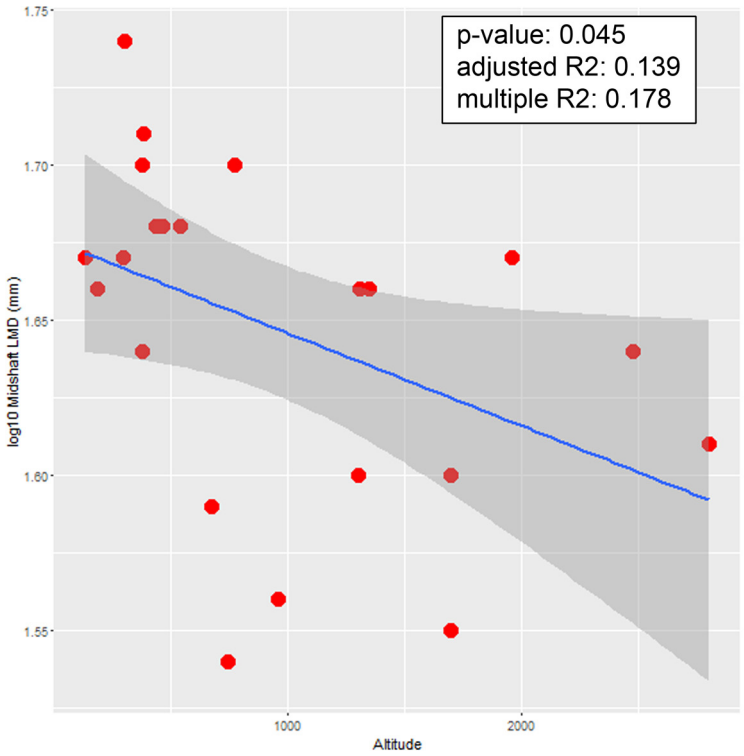
Palaeohistology and life history evolution in cave bears, *Ursus spelaeus* s.l.



Supplementary Figure 1: Variation in bone histology (medially) among different cave bear localities. White arrow heads indicate LAGs and red arrow heads LAGs within the OCL. Please note that the last red arrow heads in CuO 7528-1 and the last red arrow head in DR 35 are flipped. (Scale bars: 2 mm)



Supplementary Figure 2: Variation in bone histology (medially) among different cave bear localities. White arrow heads indicate LAGs and red arrow heads LAGs within the OCL. Please note that the red arrow heads of the OCL are flipped in PEC 1183 (Scale bars: 2 mm)



Supplementary Figure 3: Correlation between body size as expressed by log10 lateral-medial diameter (LMD) and altitude of the cave bear locality.

Chapter VI

‘Resurrecting’ Darwin’s Niata - anatomical, biomechanical, genetic, and morphometric studies of morphological novelty in cattle

Kristof Veitschegger, Laura A. B. Wilson, Beatrice Nussberger, Glauco Camenisch, Lukas F. Keller, Stephen Wroe, and Marcelo R. Sánchez-Villagra (in preparation)

Author Contributions:

KV designed and conceived the study, collected the morphological and morphometric data, performed the respective analyses, prepared the figures and tables, and wrote and reviewed the manuscript.

LABW and SW designed and performed the FEA, prepared figures and tables, and wrote and reviewed the manuscript.

BN, GC, and LFK designed and performed the genetic analyses, prepared figures, and wrote and reviewed the manuscript.

MRSV designed and conceived the study as well as wrote and reviewed the manuscript.

‘Resurrecting’ Darwin’s Niata - anatomical, biomechanical, genetic, and morphometric studies of morphological novelty in cattle

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Abstract

The Niata was a cattle variety from South America, which figured prominently in writings on evolution by Charles Darwin. Its shortened head and other aspects of its morphology have been subject of unsettled discussions since Darwin’s time. Here, we examine the anatomy, cranial shape, skull biomechanics, and molecular aspects of the Niata as an example of the evolution of morphological disparity during domestication. The Niata was a viable variety of cattle and exhibited anatomical differences to known chondrodysplastic traits. In cranial shape and genetic analysis, the Niata occupies an isolated position clearly separated from other cattle breeds. We find no evidence from computational biomechanics that the much derived skull configuration compromised the Niata’s ability to process plant matter. Morphological and genetic data illustrate the acquisition of novelty in the domestication process and confirm the distinct nature of the Niata cattle, validating Darwin’s view that it was a true breed.

Keywords: brachycephaly, shapes, morphospace, sutures, Finite Element Analysis (FEA), single nucleotide polymorphism (SNP)

The Niata

The change in skull shape towards a short and stout appearance (brachycephaly) is an independently reappearing trait during domestication and is considered a breed-defining characteristic in some dogs, cats, and pigs [1]. In cattle, extreme brachycephaly has only been described in the Niata cow from South America (Figure 1). The first documented encounters with the Niata are from the early 19th century [2, 3]. However, the Niata only received widespread recognition after the publication of Charles Darwin's second edition of the Journal of Researches in 1845 [4]. Darwin described the appearance of the Niata and discussed its evolution, existence, and biology. The Niata became a controversial subject among scientists in Europe, especially France. It was unheard of that cattle could develop such a skull configuration and still be considered a true breed and not a malformation [5-13] This is a false dichotomy still found in literature today [1, 14]. Lenient definitions of breeds simply require the human intend to select for and preserve certain morphology within a species that distinguishes this population from other members of the species [1].

Although the peculiarities of the Niata have been widely discussed, the issues raised since Darwin's writings have not been solved. We aim to do so with several approaches. We investigate the anatomy and body size of the Niata and evaluate the first description of its skull by Owen [15]. Additionally, we use geometric morphometrics of the skull and genetic data to place the Niata within the context of other cattle breeds. We test for the existence of intermediate shapes between the extreme brachycephaly of the Niata and more regular shapes as found in e.g., Simmentaler cattle.

The morphology of the Niata has been tied to disease and malformations [11]. Dareste made the first connection between chondrodysplastic bulldog-calves, also known as snorter dwarfs, and the Niata cattle [6]. Chondrodysplasia is a congenital disease, which leads to shortened limbs, brachycephalic skulls, and an early fusion of the spheno-occipital synchondrosis in cattle and often times is lethal [16, 17]. However, mutations in genes associated with chondrodysplasia can also be important drivers in the appearance of breeds [18] and in dogs different genes are related to chondrodysplasia and brachycephaly, respectively [18, 19]. In cattle, several genes such as ACAN, PRKG2, and EVC2 are considered to be related to so-called snorter dwarf-like chondrodysplasia [17, 20, 21], which is even breed defining in Dexter cattle [17]. Here, we examine the cranial and postcranial morphology of the Niata to compare it with anatomical markers for chondrodysplasia in cattle.

For Darwin, the Niata was an illustrative example for selection [4]. He was convinced that the Niata must have experienced disadvantages during droughts because its extreme brachycephaly, resulting in a projecting lower jaw, should have negatively affected the process of feeding. We explore biomechanics to address feeding in the Niata by using Finite Element Analysis (FEA) to look at

Figure 1: Reconstruction of cranial muscles and external head morphology of the Niata based on the skull MLP 1126. Artwork by Jorge González.

the stress distribution over the Niata skull and compare it to other types of cattle.

We extracted DNA from Niata specimens in museum collections to study single nucleotide polymorphisms (SNPs). Niata characteristics have been described in several cattle breeds [6, 22, 23]. We test the clustering of Niata individuals and their relations to indicine Zebu breeds, taurine European breeds, hybrids, and *Bos javanicus* [24].

Results

Cranial and postcranial anatomy

The skull of the Niata is short and broad, as is typical for a brachycephalic condition (Figure 2, see supplementary information for measurements). The maxillary bone of the Niata has a triangular outline due to the close approximation, or direct contact, of lacrimal and premaxillary bone. It is shortened and the facial crest cannot be easily distinguished; the facial tuber is very prominent. The alveolar process towards the teeth is convex and the diastema is shortened. The shortening of the maxillary bone has also changed the angle between premolar and molar teeth. The premolar teeth are placed in an obtuse angle to the molars as is also the case in the lower jaw. In the premaxillary bone, the alveolar process and the body of the incisive bone are short and stout. The premaxillary bones are medially curved upwards so that the process is V-shaped from anterior view. The nasal process is variable in length, but in three of the five examined skulls, it comes into contact with the lacrimal bone. The shortening of the maxillary bone, therefore, slightly changed the configuration of the sutures in the skull. The nasal bones of the Niata are short, stout, and are convex in lateral view. The

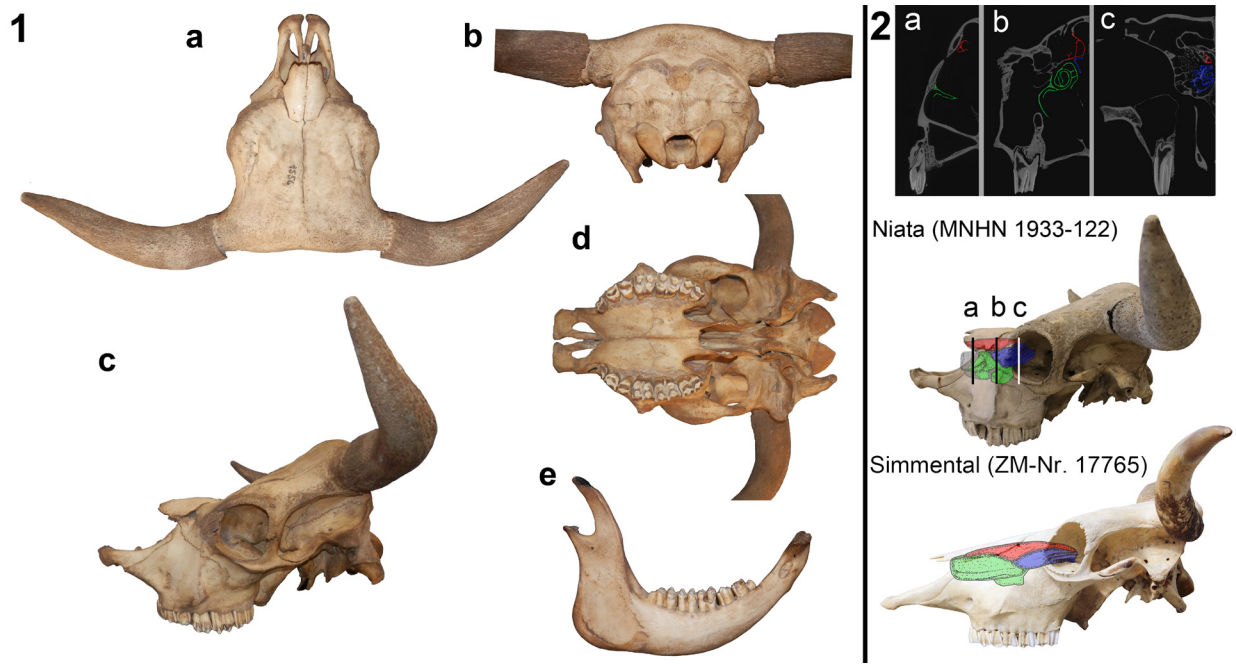

Figure 2: Skull and lower jaw of the Niata (MLP 1556). 1a: skull dorsal view, 1b: skull posterior view, 1c: skull lateral view, 1d: skull ventral view,1e: lower jaw lateral view. 2: schematic reconstruction of the dorsal (red), middle (blue), ventral (green) conches in the Niata (broken parts are reconstructed in grey) based on CT scan data (mirrored).

suture between the two nasal bones fuses in the Niata and in one of the examined specimens it was not visible anymore. Due to the shortening of the snout region, the dorsal, middle, and ventral nasal conchae have become proportionally short and stout (Figure 2). No conch has been affected more strongly than any other. The frontal bone of the Niata is curved upwards to the nasal bones. The intercornual protuberance can be from W-shaped to flat in dorsal view. The length of the frontal bone from the nasal-frontal suture in midline (nasion) to the posterior edge of the skull in midline (acrocranion) is rather short compared with the smallest length of the frontal bone. This gives the frontal bone a squarish appearance. At the base, the bony part of the horns of the Niata grows in lateral direction and then turns antero-dorsally. In individuals with longer horns, a second turn to postero-dorsal can be observed. The orbits of the Niata are square-shaped and, due to the shortening of the snout, placed more anteriorly. The jugal bone and the lacrimal bone are shortened towards the maxillary bone. The morphology of the occipital bone and temporal fossae do not differ between the Niata and other breeds. The craniobasal angle of the Niata is over 180° or airorhynch condition. The lower jaw is curved upwards and the incisors project over the body of the incisive bone of the premaxillary bone, leading to malocclusion [4].

The external suture obliteration pattern of the cranial sutures of the Niata is not different from that observed in other cattle (Figure 3). The Niata skull with the oldest individual age (MLP 1126), however, shows a high degree of external suture obliteration. The spheno-occipital synchondrosis remained open in a

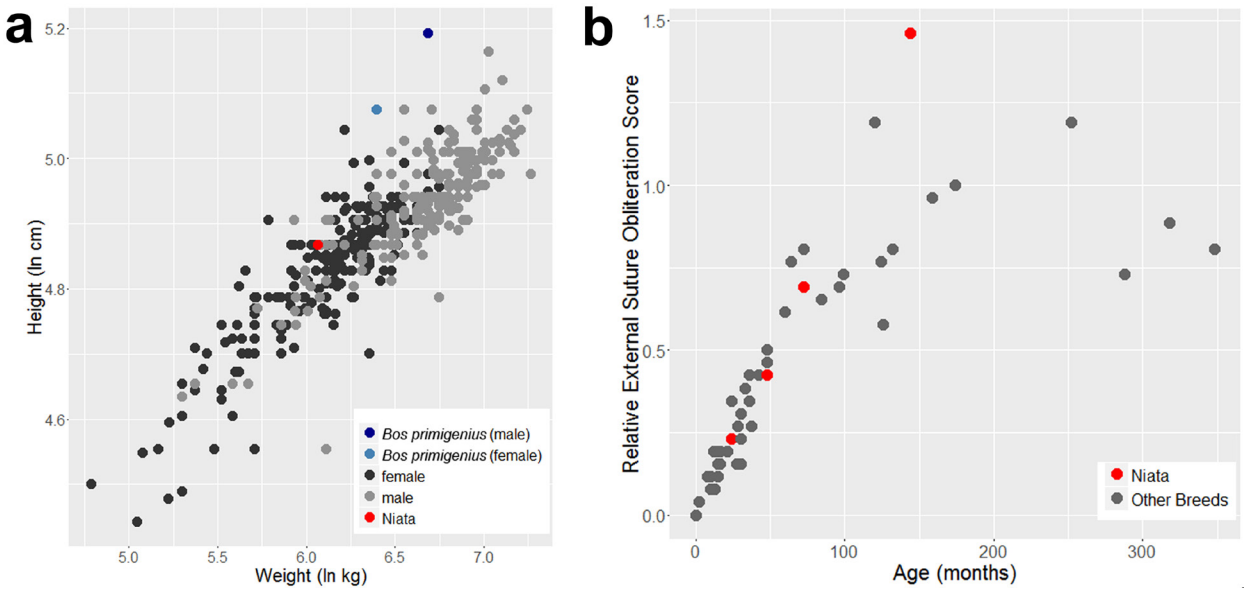

Figure 3: a: Body size of the Niata cattle compared to other taurine cattle breeds. b: Relative external suture obliteration scores at different ages in the Niata and other cattle breeds.

specimen with an estimated age of about 24 – 30 months based on the shedding of deciduous teeth [25]. All other Niata specimens exhibit a fused spheno-occipital synchondrosis and permanent dentition.

The Niata was of average size when compared to other taurine breeds (Figure 3). The body mass of the Niata was reconstructed based on the complete skeleton MLP 1126, a male [26]. The comparison of the ratio of limb length and cervical-sacrum length among breeds shows that the Niata did not have short limbs compared to its body length, nor are the hindlimbs disproportionally longer than the forelimbs (Supplementary Figure 5 & 6).

Morphometric analysis

The landmark-based morphometric analysis of the skulls clearly shows a distinction between the Niata and other breeds (Figure 4). Principal component (PC) 1 accounts for 34.9 percent of the overall shape variation and is defined by the difference between short skulls (brachycephalic) and elongated ones (dolichocephalic), as found in Sanga and Zebu cattle. The second PC axis shows similar shape changes as the first one, but less pronounced. Here, the difference relates to the angle between the nasal and frontal bones as well as the broadness of the skull. This axis accounts for 9.4 percent of the shape variation. The third PC axis accounts only for 7.9 percent of the shape variation and is mainly defined by extension of the nasal process of the premaxillary bone. No further PC axis accounts for more than five percent of the shape variation in the sample. Overall, the Niata is located away from other breeds in morphospace, evidenced by large Procrustes distances (PD) for pairwise comparisons. The mean shape of a Niata skull is most different from Bucharan Grey (PD: 0.29), Sanga (PD: 0.26), and Zebu (PD: 0.25) cattle and closest to Tuxer (PD: 0.15), Zillertaler

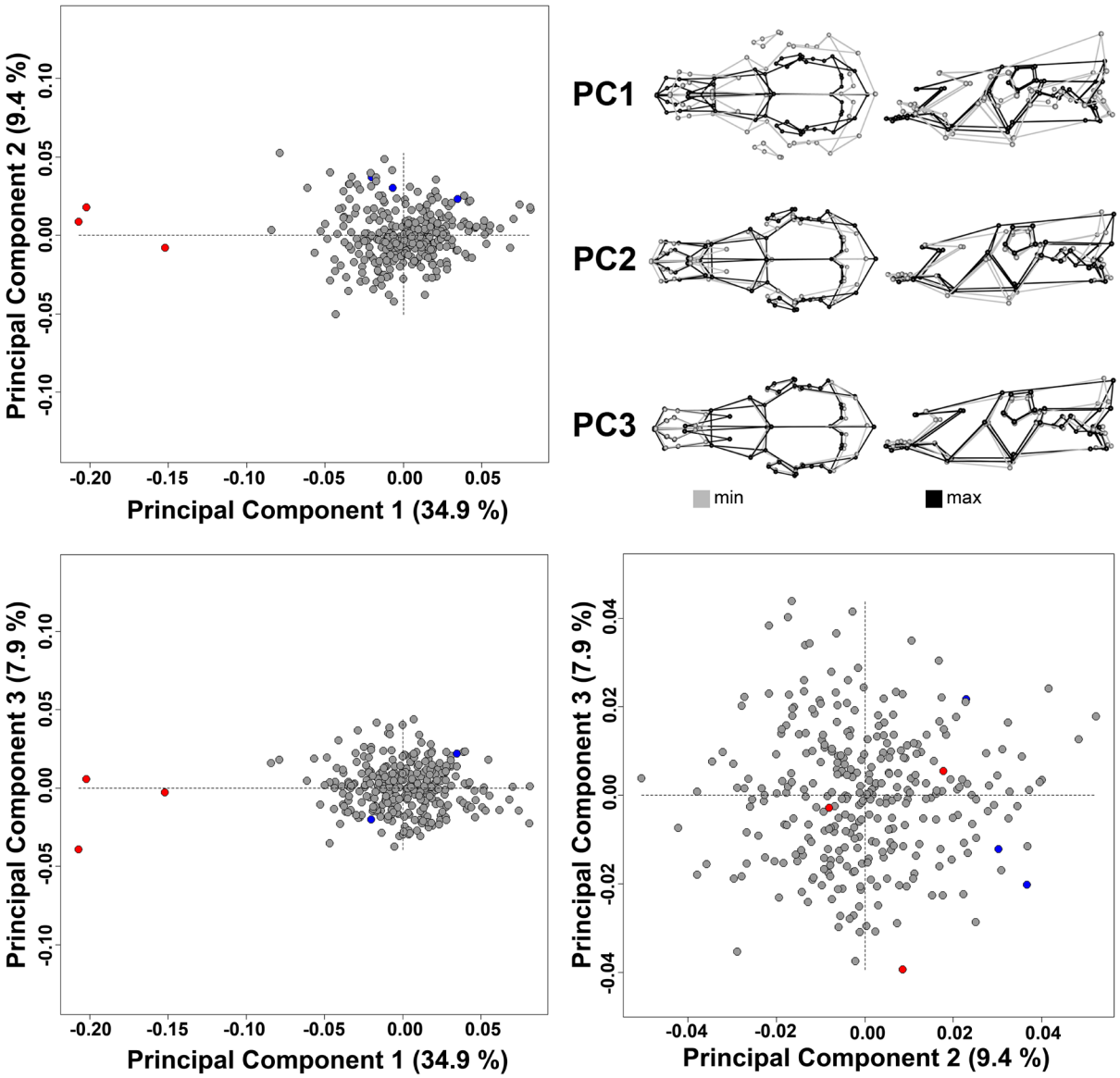

Figure 4: Principal Component Analysis of the skull shapes of different cattle breeds. Top left, bottom left and bottom right are the comparisons between PC1, PC2, and PC3. Top right are the associated shape changes. Numbers in parentheses indicate shape variation explained by respective PC axes. Red dots indicate the Niata and blue dots the aurochs (*Bos primigenius*).

(PD: 0.17), as well as Jersey (PD: 0.17) cattle. In comparison, Maas-Rhein-Ijsselschlag cattle, a breed closer to the mean shape, is most different in shape to the Niata (PD: 0.21), the Bucharan Grey (PD: 0.11), and the Tuxer (PD: 0.08) cattle and more similar to the Devon (PD: 0.02), North Wales (PD: 0.02), and Bohemian Red (PD: 0.02) cattle. A similar pattern was recorded for the lower jaw (Supplementary Information).

Finite Element Analysis

Von Mises (VM) stress was estimated because it is a good indicator of mechanical performance in materials that fail under a ductile model of fracture [27] and muscle forces were scaled according to body mass for each specimen. In general, the VM stress contour maps indicate broad similarities in the distribution of VM stress across all three investigated breeds: Niata, Simmentaler, and Zebu.

Across all loading cases, the Niata cranium exhibited comparatively low stress levels, particularly across the dorsal surface of the frontal and the supraorbital sulcus (Figure 5 G, H). Compared to the Simmentaler and Zebu, the Niata cranium showed lower stress along the lateral margin of the frontal and squamosal (Figure 5, lateral models A, C, E). All breeds showed high VM stress values along the zygomatic arch for all loading cases.

For the unilateral bite, all breeds showed greater VM stress values in the rostrum on the working-side compared to the balancing-side (unloaded), especially for the maxilla and lacrimal region, as well as slightly increased stress for the working-side compared to the balancing-side dorsal surface of the frontal (Figure 5, H, J, L). Comparing the VM stress contour maps for the working-side unilateral bite and the bilateral bite in lateral view, for all breeds the results show that the unilateral bite leads to increased VM stress in the anterior portion of the maxilla and near to the suture between the maxilla and zygomatic (Figure 5). Compared to Zebu and Simmentaler, the Niata displays only a slight increase in magnitude and extension in distribution of VM stress near to the maxillo-zygomatic suture (Figure 5 A-B).

Consistent with the contour map results, strain results collected at the temporomandibular joint (TMJ) for the unilateral loading case indicated that overall the Niata cranium showed the lowest VM strain values (218.05-218.76 με; Supplementary Table 12). The difference between VM strain values for the working-side TMJ compared to the balancing-side TMJ was lowest for the Niata (0.32%), and highest for the Zebu (9.5%) (Supplementary Table 12). The predominant mode of strain at the TMJ was compressive.

Among the breeds, the Niata exhibited overall lower VM stress along the mid-sagittal plane of the cranium (average=0.31 MPa; Simmentaler, average = 0.37 MPa; Zebu, average = 0.50 MPa)(Supplementary Figure 12, A). The difference in stress between the Niata and the other breeds was most conspicuous at points 3-6 for the bilateral bite, corresponding to the area extending from the posterior part of the nasal, beyond the naso-frontal suture, towards the orbits. Along the dorsal midline, the Niata displayed more variation in stress values between the unilateral and bilateral bite than Zebu and Simmentaler, particularly showing greater stress in the unilateral bite for points 4-8 (Supplementary Figure 12, A).

Overall the pattern of VM stress values was more similar among the breeds along the tooth row than along the dorsal midline (Supplementary Figure 12). VM stress values were, on average, higher for the tooth row equidistant points (0.51-0.68 MPa) compared to those collected along the mid-sagittal plane (0.27-0.50 MPa). For all breeds, differences between the bilateral and unilateral bite were generally most marked towards the anterior portion of the tooth row, corresponding to points 1-5 (Supplementary Figure 12, B). The Simmentaler and Zebu displayed greater

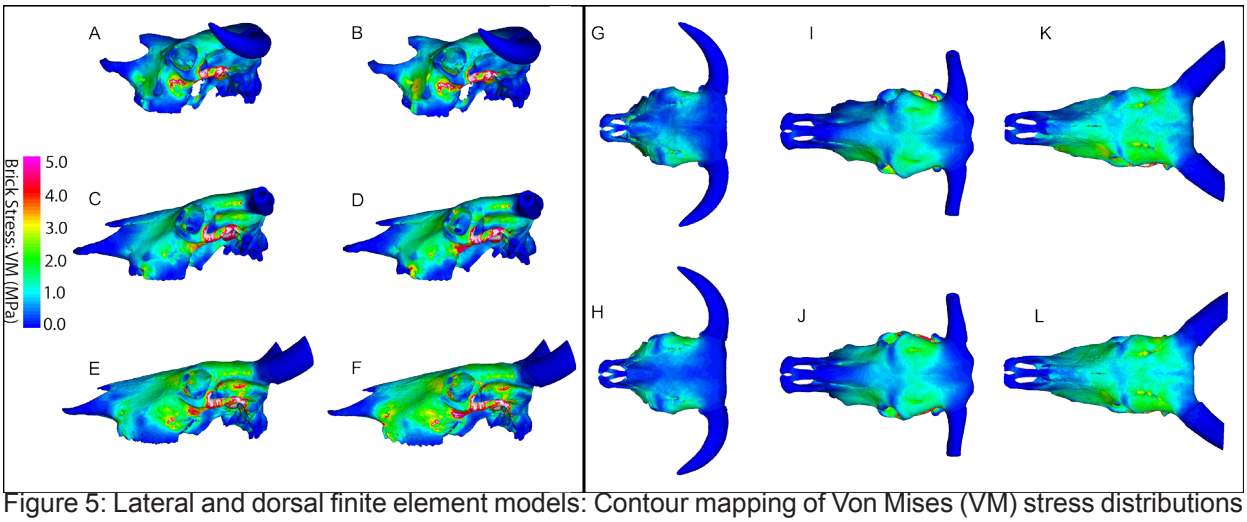

Figure 5: Lateral and dorsal finite element models: Contour mapping of Von Mises (VM) stress distributions in lateral view. Models were subjected to loading cases simulating a bilateral anterior bite (A, C, E, G, I, K), and a unilateral anterior bite (B, D, F, H, J, L). Models are for Niata (A, B, G, H), Simmentaler (C, D, I, J) and Zebu (E, F, K, L). Muscle forces were scaled to body mass for each model. White regions exceed the scale.

differences between stress values for the bilateral bite and unilateral bite along the tooth row than the Niata.

Analysis of SNP data

Using data from 2,205 SNP loci genotyped in this study in five Niata samples and in 134 other cattle breeds by Decker et al. [24], it is evident that Niata cattle form a genetic cluster that belongs to the taurine breeds. Both principal component analysis (Figure 6) and phylogenetic analysis (Supplementary Figure 13, Supplementary Figure 14) confirm this view. Of all the breeds included in our analyses, Niatas cluster furthest away from the indicine breeds. Furthermore, Niata samples do not cluster with Iberian breeds (e.g., Morucha) or South American breeds (e.g., Corriente), nor with breeds known for the occurrence of some forms of chondrodysplasia (e.g., Dexter, Angus, Hereford, Kerry) [14, 16, 17, 20]. Instead, they form their own, independent cluster, suggesting that Niata can be considered a separate breed. However, one of the Niata samples (MACN-Ma 25.162) clustered between European and American breeds, and may not represent the same gene pool as the other Niata samples. We could not determine the closest relative of the Niata breed because the exact branch location of Niata was not reproducible in phylogenetic analyses with different parameters (Supplementary Figure 13, Supplementary Figure 14).

Discussion

Anatomical evidence and signs of chondrodysplasia

The Niata exhibits a brachycephalic skull and reveals morphological and biomechanical singularities. Suture configurations in some individuals diverge from the norm for cattle, as the lacrimal bone coming into contact with the premaxillary bone, although this is not universal in Niata skulls (contra [15]). We found a transition in the basicranial angle

from an ancestral condition of around 158°, as found in the aurochs (*Bos primigenius*) [14], to an angle of about 193° in the Niata. All examined breeds fall within these two extremes. The pattern in dogs is different: the wild ancestor of dogs, the grey wolf (Canis lupus), has a basicranial angle of about 170°, in the middle of the range between the Barsoi (158°) and the French bulldog (183°) breeds [28, 29]. The spheno-occipital synchondrosis in the Niata has not been affected by the change in the skull configuration. This is of particular importance, as an early fused synchondrosis has been shown to be characteristic for chondrodysplastic malformations in cattle. In individuals affected with the snorter dwarf condition the synchondrosis fuses at around 5.5 months [16]. In dogs, brachycephalic breeds are more likely to have a relatively early closed spheno-occipital synchondrosis [30]. Generally, the external suture obliteration pattern of the Niata is within the range of other cattle of similar age until the age of 72 months. The oldest skull (MLP 1126) has the highest external suture obliteration score within the dataset. This is in agreement with a pattern found in brachycephalic dogs [29]. However, external suture obliteration patterns are more variable in older cattle [31]. Sutures have an important role in mitigating stress on the skull, therefore an early fusion can lead to irregular bone growth [32]. Despite the many different changes to the skull, the body size and limb proportions of the Niata show no delineations from other cattle. In contrast, in Dexter short limbs are one of the breed defining characteristics [17]. The average proportions of Niata do not support early reports of disproportionally short front limbs (Supplementary Figure 5) [4].

Geometric morphometrics and genetic evidence

The Niata occupies a unique position in the morphospace of cattle skulls, as evidenced by large Procrustes distances revealed in the morphometric analysis. The breeds most similar to the Niata in skull shape are the Tuxer and Zillertaler. Early works reported similarities between the Tuxer and the Niata [33, 34]. Another similar breed similar is the Jersey [14] which, like the Niata, has an upward curved forehead. The furthest removed from the Niata skull shape are the Bucharan Grey, followed by Zebu and Sanga cattle. Zebu and Sanga are dolichocephalic breeds, which originated from another domestication center than most European breeds [35]. The first cattle that were brought to the Americas were from Iberian taurine origin and intermixture with indicine breeds did not happen before the mid-19th century [36]. Based on this knowledge of the origin of South American cattle breeds [37-39], it is of particular interest that the Niata does not cluster with any Iberian breed within the dataset such as the Tudanca or Rubia Gallega. The distinct position of the Niata is confirmed in the PCA based on SNP data (see below). Here, the Niata individuals form a cluster that slightly overlaps with the taurine breeds (Figure 6).

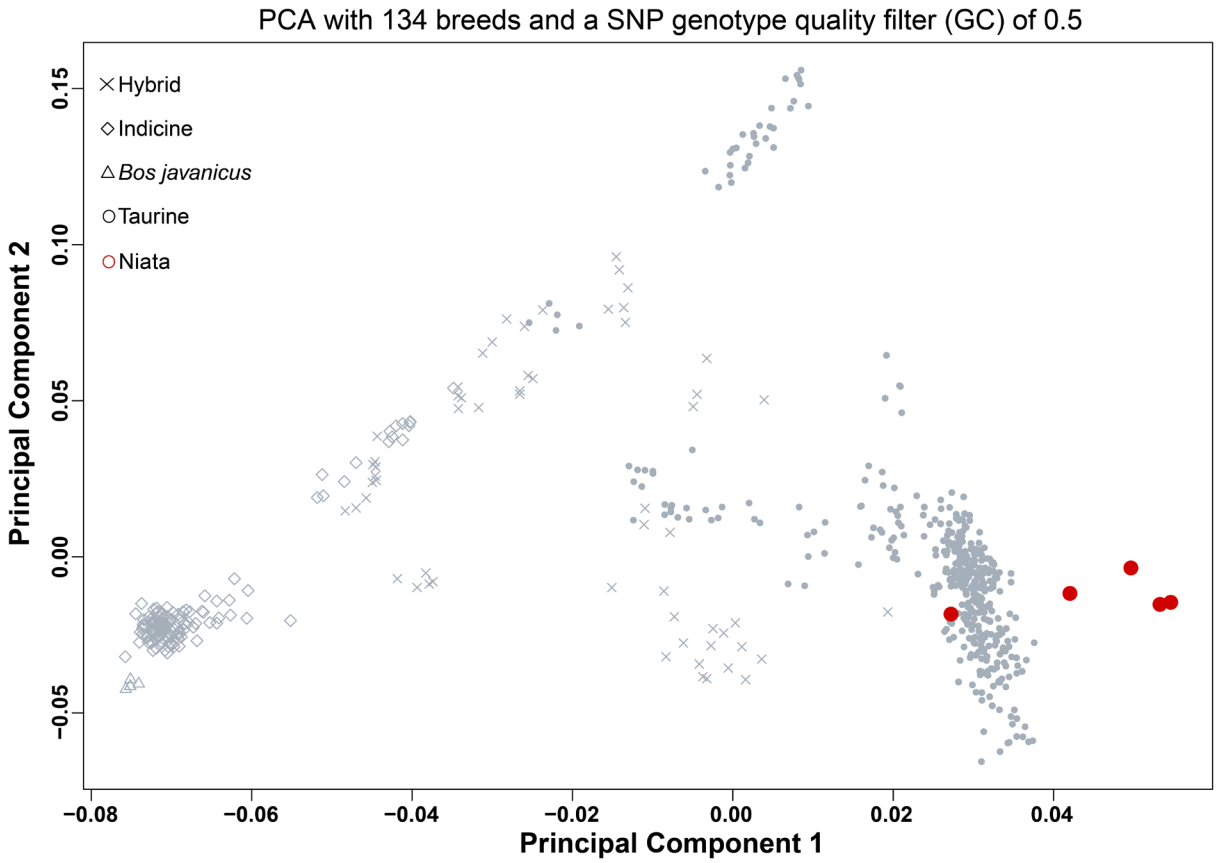

Figure 6: Principal Component Analysis of genotypes based on 2'505 SNPs, with Niata genotype quality score of GC 0.5. Niata are compared to other cattle breeds (data from Decker et al. 2014).

Finite element analysis

Darwin suggested that the Niata had a disadvantage compared to other cattle breeds when foraging. He stated that the protruding lower jaw of the Niata inhibits it from properly browsing twigs or reeds in case of droughts, thus leading to its demise [4]. There is no preserved soft tissue of the lips of the Niata, nor is there any depiction of a feeding Niata that would allow us to determine precisely what effect the protruding lower jaw had on the process of feeding. However, from our FEA results there is no evidence to suggest that mechanical performance was compromised. Indeed the skull of the Niata, which experienced less stress during both anterior bilateral biting and unilateral molar biting than the other breeds considered.

The Niata in context of breeds

The origin and fixation of the Niata traits in South American cattle was most likely not intentional but rather a result of a very small founding population [38]. Darwin [4] already wrote about the heritability of the Niata traits and he asserted that the breed is true. However, evidence for the inheritability of the Niata traits comes from breeding experiments in Jersey cattle [22]. These experiments also showed that heavily brachycephalic cattle suffer from inheritable impaired vision [22]. Inherited illnesses are a common phenomenon in several modern dog and cat breeds [40]. The Niata is an illustrative case on how domestication can expand the

morphospace of a species. In cattle, however, 'extreme' or very derived anatomical traits appear to be discriminated against, which may be due to the utility value of cattle, e.g., being efficient dairy and meat producers as well as work animals [1, 41]. Therefore, a breed with possible inherent health problems and probably difficult temper, as stated by Darwin, would be less appreciated [4, 22]. This aspect of selective breeding can be easily exemplified by the different perception and recognition of heavily brachycephalic dogs such as French bulldog or the Boxer as true breeds [1] whereas the status of the Niata as breed has been controversial. Early works dismissed the possibility of such a breed completely [11] and in recent years it still was described as a defective form [14]. However, following a standard breed definition [1] (p. 40): "A breed is a group of animals that has been selected by humans to possess a uniform appearance that is inheritable and distinguishes it from other groups of animals within the same species," the Niata can be considered a breed. Our genetic and morphometric evidence clearly shows the distinctiveness of the Niata as true breed as suggested originally by Darwin [4]. The case of the Niata, which vanished sometime in the late 19th or early 20th century [26, 42], is an example for the trend of extinction of breeds of domesticated forms of several species and thus loss of genetic diversity [43].

Material and Methods

Cranial and postcranial anatomy

Skull measurements were taken according to von den Drisch [44] and skull terminology follows Budras et al. [45]. We used a µCT scan from the skull MNHN 1933-122 to assess the change of the configurations of the nasal conches. CT-scan of the Niata skull MNHN 1933-122 was carried out with a Phoenix v|tome|x L 240-180 at the AST-RX platform, MNHN, Paris, France (http://www.ums2700.mnhn.fr/ast-rx/acces).Following parameters were used: voltage 220 kV, current 300 mA. The scan resulted in 3053 images with a voxel size of 0.12357352 mm (exposure time 500 ms). Phoenix x-ray datos|x software was used to export a 16 bit TIFF image stack. Manual segmentation of the nasal conchae was performed in Avizo 8.1.

The pattern of external suture obliteration in 26 sutures was documented in 47 cattle skulls of known age (Supplementary Table 3). Not all skulls in this comparative dataset had breed information. Additionally, we studied four skulls of Niata cattle (Supplementary Table 3). The age of the Niata specimens was estimated based on tooth eruption, incisor wear pattern as well as information from literature [25, 26]. External suture obliteration was documented in three stages. A suture was open when no signs of obliteration were visible; this was scored as "0". Any degree of closure was scored as "1" and a completely obliterated suture was scored as "2". The overall average of the scores was compared with individual age. Basicranial angle was measured in 77 skulls from 36 breeds (Supplementary

Table 2). Four landmarks were used to measure the basicranial angle: suture between premaxillary and maxillary bone in the midline (1), tip of the palatine bone in midline (2), suture between vomer and presphenoid in midline (3), and ventral border of the foramen magnum in midline (4). These four landmarks were visualized in lateral view using Morphologika 2.5 [46]; a wireframe was drawn between landmark 1 and 2 as well as landmark 3 and 4. The angle was measured between these two lines. Resulting angles were averaged per breed. The body mass of the Niata was calculated by using and averaging different cranial and postcranial measurements; see supplementary information [47-49]. The height of the Niata was taken from Baldassarre [26]. The resulting average weight and the height were compared with those of 264 different taurine breeds (208 male and 262 female) as well as the aurochs, *Bos primigenius* (Supplementary Table 13). The comparative data for height and weight were taken from Felius [14].

Morphometric analysis

The data were obtained using a Microscribe digitzer (Microscribe MX, Immersion Corporation, San Jose CA) by the first author. 53 landmarks were used to capture the shape of the whole skull. Custom frame was used in MUS 6.0.1 to digitize the dorsal and ventral part of the skull. Twelve landmarks were used to analyze the general shape of the left half of the lower jaw. The shape of the cattle skulls and lower jaws was analyzed using geometric morphometrics [50-52]. All analyses were performed using the package geomorph [53] as implemented in R, version 3.2.3 [54]. Initially, a Generalized Procrustes Analysis was performed to align the specimens and remove size [55]. We used centroid size to remove a possible effect of allometry in our dataset [53]. After creating the so called allometry-free shapes, we performed a Principal Component Analysis. At the beginning of data collection, one skull and one lower jaw were digitized five times to estimate error of precision [46]. Observer error was small compared to the variation within the dataset. To assess the degree of morphological difference between the Niata skull shape and other breeds, we calculated the Procrustes distance between mean skull shapes of breeds. Procrustes distance is the least squared mean distance between shapes after Procrustes alignment [55]. Altogether, the final dataset consisted of 316 adult skulls representing 86 breeds (including 4 landraces, 7 crossbreeds, 4 Zebu varieties, 2 Sanga breeds, and *Bos primigenius*) as well as 238 adult lower jaws from 65 breeds (including 1 landrace, 1 crossbreed, 2 Zebu varieties, 1 Sanga breed, and *Bos primigenius*).

Finite Element Analysis

Computed tomography scan data: Finite Element Models (FEMs) were constructed from computed tomography (CT) scan data collected for three specimens. These were, Niata MLP 1126 (slice thickness = 0.67 mm, inter-slice distance = 0.33 mm) provided by Alfredo A. Carlini, Diego H. Verzi, and Itatí A. Olivares (Museo de La

Plata); Simmentaler ZMUZH 17765 (slice thickness = 1.00 mm, inter-slice distance = 0.20 mm) and Zebu ZMUZH 17767 (slice thickness = 1.00 mm, inter-slice distance = 0.20 mm). Niata MLP 1126 was scanned at the Centro de Imágenes Médicas (CIMED), La Plata, Argentina with the CT scanner Scan Phillips Brilliance 64 with a current of 229mA and a voltage of 120 kV. 1943 images were created and exported as DICOM stack with implemented software version 2.6.2. The voxel size was 0.976563 mm and exposure time was 655 ms. The Simmentaler and Zebu skulls were scanned at the Universitätsspital Zürich, Zürich, Switzerland with a Siemens SOMATOM Force CT-scanner using a voltage of 120 kV and a current of 132 mA. The exposure time for both skulls was 1000 ms. The Simmentaler scan consisted of 2850 images and had a voxel size of 0.947266 mm. The Zebu scan consisted of 2750 images and had a voxel size of 0.904297 mm. The image stacks were exported as DICOM stacks using the implemented software syngo CT VA50A.

Estimation of body mass and muscle force: Body mass (BM) for each specimen was estimated using measurements of the lower molar tooth row length (LMRL), second lower molar length (SLML), anterior jaw length (JLB) and posterior jaw length (JMA), following the equations developed on ungulates by Mendoza et al. [56], where:

BM = -1.602LMRL + 2.791SLML + 0.576JLB + 1.005JMA + 2.402

Postcranial material was available for MLP 1126, allowing body mass to be estimated from the circumference of the femur and humerus for this specimen, following the equation for quadrupedal mammals presented by Anderson et al. [48] and from measurements of the humerus, following the bovid-specific equations of Scott [47]. The average of skull and postcranial body mass estimates was used for MLP 1126.

The major jaw closing muscles were modelled for each specimen, their origin and insertion points were defined using a bovine anatomical atlas [45]. These were m. masseter, m. temporalis, m. pterygoideus lateralis and m. pterygoideus medialis. Muscle forces were predicted on the basis of maximum cross-sectional area (CSA) using the 'dry skull' method and CSA values were multiplied by the tension value for vertebrate striated muscle of 0.3 N/mm2 [57, 58]. The CSA values were summed for the four muscle groups, and the relative proportion of each muscle was calculated; these data were compared to muscle mass values for ungulates [59]. Muscle forces were distributed in each model based on the percentage contribution of each muscle group to the total (Supplementary Table 11).

Muscle forces were scaled according to body mass for each specimen [60]. When a body is scaled geometrically by a factor of k in all dimensions, the volume of the body scales by k3 whereas the muscle cross-sectional area of the body scales by k2; this can be expressed in the following, two-thirds power scaling equation:

MFtarget / MFref = (BMtarget/BMref)^2/3

Where MFtarget is the muscle force of the target specimen (to be calculated), MFref is the muscle force of the reference specimen, BMtarget is the body mass of the target specimen, and BMref is the body mass of the reference specimen [61, 62]. We used the Niata MLP 1126 model as MFref to estimate MFtarget for the Simmentaler and Zebu models, using the above equation.

Finite Element Model (FEM) assembly: Three-dimensional (3D) surface meshes were created from DICOM image stacks using Mimics (Materialize, Version 18.0), and volume meshing was performed in 3-Matic (Materialize, Version 9.0). Volume meshes were imported as Nastran (NAS) files into Strand 7 v. 2.4.5 (Strand 7, Pty Ltd, Sydney, NSW) for Finite Element Model (FEM) assembly (Supplementary Figure 11). Each model comprised 1.5-1.8 million 4-noded tetrahedral (tet-4) 'brick' elements: Niata MLP 1126 - 1,781,890 bricks; Simmentaler 17765 – 1,552,228 bricks; Zebu 17767 – 1,594,008 bricks. Following previous protocols for comparative Finite Element Analysis (FEA), all FEMs were homogeneous and tet-4 elements were assigned a single material property for cortical bone with a Young's modulus (E) of 13.7GPa and a Poisson's ratio (v) of 0.4 [61, 63]. Muscle architecture was modelled in 3D using multiple pre-tensioned trusses (axial-loaded beam elements), to simulate the basic geometry of muscle fibers (total 70 trusses per model). Each muscle group was represented by the same number of trusses in each model, and muscle forces were distributed between the trusses relative to muscle proportion values, as calculated above. For each muscle beam, a network of beams was tessellated on the surface of the model around the site of attachment to reduce the potential for stress artefacts associated with single node loadings.

Boundary conditions and loading cases for FEMs: Two intrinsic (bite transmitted) loading cases were simulated to mimic feeding, reflecting bites undertaken with maximal bite force using the skull musculature. These were: 1) a bilateral anterior bite at M1, and 2) a unilateral molar bite at M2. For both loading cases, models were restrained at the occipital condyle and an axis of rotation was created around the temporomandibular joint (TMJ). A rigid link spanning the foramen magnum was created and restrained in the global coordinate system (x, y, z restraint for translation and rotation) to prevent free motion of the model in virtual space. Restraints were also added at the mid-point, defined as the mid-length, of the upper M1, for each tooth row for the bilateral bite, and for the right hand side tooth row only for the unilateral bite. Restraints simulate occlusal and mandibular contacts and produce reaction forces at the point of restraint under muscle pull in an inferior line of action (see [64, 65] for similar protocol). For the bilateral bite, the TMJ was restrained in all directions, and the bite points on the tooth row were constrained in the vertical direction. For the unilateral bite, the working-side TMJ was constrained in all directions, and the balancing-side TMJ was constrained in the vertical and

antero-posterior directions. To spread the forces generated at the restrained single nodes, and to prevent artefacts in the distribution and magnitude of stress [66], networks of beams were tessellated around each fixed node.

Comparison of biomechanical performance: FEMs were solved in Strand 7 (version 2.4.5) using the direct sparse linear static solve scheme, and the AMD node ordering algorithm option. Prior to solving each model, the mandible was removed due to the inclusion of metal fixations in the Niata MLP 1126 specimen. Von Mises (VM) stress data were used to compare the structural integrity of the FEMs under the loading cases. Bone fails under a ductile model of fracture [67], and VM stress is the metric used to assess the yielding of ductile materials [68].

Relative mechanical performance was assessed using contour plots of VM stress distributions, generated in Strand 7 (version 2.4.5). To assess differences in stress magnitude and distribution between models, VM brick stress values were extracted at equidistant points along the mid-saggital plane of the cranium and along the margin of the tooth row for each model. At each equidistant point, VM stress values for five bricks surrounding the selected node were averaged. On each model, the selected node identity (ID) was recorded and the same node was chosen for each loading case. For mid-saggital sampling, equidistant points were selected along a line from the most anterior part of the nasal bone (point 1) to the most posterior part of the parietal (point 10). For the margin of the tooth row, equidistant points were selected along a line from the most anterior (point 1) to most posterior part (point 10) of the tooth row.

Reaction forces, recorded at the bite points and TMJ for each loading case, were extracted from each of the solved FEMs. Strain metrics were extracted at the TMJ on both the working and balancing sides of the model. These comprised von Mises strain (distortional strain or non-isometric strain), maximum principal strain (tension) and minimum principal strain (compression). Strain mode was calculated as the absolute value of maximum principal strain divided by minimum principal strain, to provide an indication of whether compression or tension was dominant at the TMJs (see [65]).

Analysis of SNP data

We collected five samples (tooth, bone or tissue) of the Niata in the Museo de La Plata (MLP) and the Museo Argentino de Ciencias Naturales (MACN) of Buenos Aires. We extracted the DNA following the protocol of Kruettli et al. [69], which includes cleaning the sample with 2% NaOCl to remove surface contamination, a 48 hours digest of pulverized material in 0.45 EDTA and 10% proteinase K, DNA isolation using QiaQuick PCR purification columns and DNA elution in EB buffer. Samples were genotyped with the GeneSeek® Genomic Profiler Bovine 150K SNP chip and gene called with the Illumina® GenomeStudio V2011.1 software. We analyzed the relationship between the Niata samples and 134 cattle

breeds, by comparing them to the cattle dataset generated by Decker et al. [24]. We selected SNPs which were called in both our and Decker and colleague's dataset and for which the genotype quality score was above 0.5 in all five Niata samples, resulting in 2'205 SNPs. Maximally five individuals per breed, the first ones in the list of samples given by Decker et al. [24], were included in the principal component analysis (PCA). PCA was implemented in PLINK 1.9 and plotted using R [54].

An ancestry graph was implemented in TREEMIX [70]. We generated additional graphs with slightly modified parameters, e.g., genotype quality filter (GC 0.5, GC0.6 or GC 0.7) or sample composition (with and without indicine breeds).

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References

1. Clutton-Brock J (1999). A natural history of domesticated mammals. 2nd edition. Cambridge: Cambridge University Press.
2. de Azara F (1801). Essais sur l'histoire naturelle des quadrupèdes de la province du Paraguay. Paris: Charles Pougens.
3. Miers J (1826). Travels in Chile and La Plata: including accounts respecting the geography, geology, statistics, government, finances, agriculture, manners and customs and the mining operations in Chile. London: Baldwin, Cradock, and Joy.
4. Darwin C (1845). Journal of researches into the geology and natural history of the various countries visited by H.M.S. Beagle round the world, under the Command of Capt. Fitz Roy, R.N. 2nd edition. London: John Murray.
5. de Quatrefages JLA (1863). Sur l'influence des milieux. Bull Soc Anthropol Paris. 4:350-2.
6. Dareste C (1867). Rapport sur un veau monstrueux. Lille: Typ. de Blocquel - Castiaux.
7. Dareste C (1867). Sur le mode de production de certaines races d'animaux domestiques. C R Hebd Seances Acad Sci. 64:423-6.
8. Dareste C (1867). Nouvelle réponse aux objections de M. Sanson sur un mémoire concernant l'origine tératologique de certaines races d'animaux domestiques. C R Hebd Seances Acad Sci. 64:1101-3.

9. Sanson A (1869). Sur les boeufs dits Niata de l'Amérique méridionale. Rec Med Vet. 6(4):307-8.
10. Sanson A (1867). Note sur l'origine tératologique attribuée à certaines ràces d'animaux domestiques. C R Hebd Seances Acad Sci. 64:669-70.
11. Sanson A (1867). Note sur les caractères de l'espèce et de la race et sur la non-existence d'une race de boeufs dit niata. C R Hebd Seances Acad Sci. 64:822-4.
12. Sanson A (1890). L'espèce et la race en biologie générale. Paris: Schleicher frères.
13. Baron R (1887). La race Ñata. Rec Med Vet Ec Alfort. 5:70-9.
14. Felius M (1995). Cattle breeds: an encyclopedia. Doetinchem: Misset.
15. Owen R (1853). Descriptive catalogue of the osteological series contained in the museum of the Royal College of Surgeons of England, Vol. II: Mammalia Placentalia. London: Taylor and Francis.
16. McKinley LJ, Steele WT, Hage TJ, Gregory PW (1957). Premature closure of the spheno-occipital synchondrosis in the horned Hereford dwarf of the "short-headed" variety. Am J Anat. 100:269-87.
17. Cavanagh JAL, Tammen I, Windsor PA, Bateman JF, Savarirayan R, Nicholas FW, Raadsma HW (2007). Bulldog dwarfism in Dexter cattle is caused by mutations in ACAN. Mamm Genome. 18(11):808-14.
18. Parker HG, VonHoldt BM, Quignon P, Margulies EH, Shao S, Mosher DS, Spady TC, Elkahloun A, Cargill M, Jones PG, Maslen CL, Acland GM, Sutter NB, Kuroki K, Bustamante CD, Wayne RK, Ostrander EA (2009). An expressed fgf4 retrogene is associated with breed-defining chondrodysplasia in domestic dogs. Science. 325(5943):995-8.
19. Bannasch D, Young A, Myers J, Truvé K, Dickinson P, Gregg J, Davis R, Bongcam-Rudloff E, Webster MT, Lindblad-Toh K, Pedersen N (2010). Localization of canine brachycephaly using an across breed mapping approach. PLoS ONE. 5(3):e9632.
20. Koltes JE, Mishra BP, Kumar D, Kataria RS, Totir LR, Fernando RL, Cobbold R, Steffen D, Coppieters W, Georges M, Reecy JM (2009). A nonsense mutation in cGMP-dependent type II protein kinase (PRKG2) causes dwarfism in American Angus cattle. PNAS. 106(46):19250-5.
21. Murgiano L, Jagannathan V, Benazzi C, Bolcato M, Brunetti B, Muscatello LV, Dittmer K, Piffer C, Gentile A, Drögemüller C (2014). Deletion in the EVC2 gene causes chondrodysplastic dwarfism in Tyrolean Grey cattle. PLoS ONE. 9(4):e94861.
22. Becker RB, Arnold PTD (1949). "Bulldog Head" cattle: Prognathism in grade Jersey strain. J Hered. 40(10):282-6.
23. Duerst U (1931). Grundlagen der Rinderzucht. Berlin: Julius Springer.
24. Decker JE, McKay SD, Rolf MM, Kim J, Molina Alcalá A, Sonstegard TS, Hanotte O, Götherström A, Seabury CM, Praharani L, Babar ME, Correia de Almeida Regitano L, Yildiz MA, Heaton MP, Liu WS, Lei CZ, Reecy JM, Saif-Ur-Rehman M, Schnabel RD, Taylor JF (2014). Worldwide patterns of ancestry, divergence, and admixture in domesticated cattle. PLoS Genet. 10(3):e1004254.
25. Habermehl K-H (1975). Die Altersbestimmung bei Haus- und Labortieren. 2., vollständig neubearbeitete Auflage. Berlin und Hamburg: Paul Parey.
26. Baldassarre S (1906). La Zootecnia nella repubblica argentina. Atti del Reale Istituto d'Incoraggiamento alle Scienze Naturali di Napoli. 6(58):359-80.
27. Dumont ER, Piccirillo J, Grosse IR (2005). Finite-element analysis of biting behavior and bone stress in the facial skeletons of bats. Anat Rec A Discov Mol Cell Evol Biol. 283A(2):319-30.
28. Nussbaumer M (1982). On the variability of dorso-basal curvatures in skulls of domestic dogs. Zool Anz. 209(1-2):1-32.

29. Geiger M, Haussman S (2016). Cranial suture closure in domestic dog breeds and its relationships to skull morphology. Anat Rec. 299(4):412-20.
30. Schmidt MJ, Volk H, Klingler M, Failing K, Kramer M, Ondreka N (2013). Comparison of closure times for cranial base synchondroses in mesaticephalic, brachycephalic, and cavalier king charles spaniel dogs. Vet Radiol Ultrasound. 54(5):497-503.
31. Ussow SS (1901). Ueber Alters- und Wachstumserănderungen am Knochengerüst der Haussäuger. Archiv für wissenschaftliche und praktische Tierheilkunde. 27:339-94.
32. Moazen M, Curtis N, O'Higgins P, Jones MEH, Evans SE, Fagan MJ (2009). Assessment of the role of sutures in a lizard skull: a computer modelling study. Proc Biol Sci. 276(1654):39-46.
33. Adametz L (1926). Lehrbuch der allgemeinen Tierzucht. Wien: Julius Springer.
34. Wilckens M (1876). Die Rinderrassen Mittel-Europas. Grundzüge einer Naturgeschichte des Hausrindes. Berlin: Paul Parey.
35. Gibbs RA, Taylor JF, Van Tassell CP, Barendse W, Eversole KA, Gill CA, Green RD, Hamernik DL, Kappes SM, Lien S, Matukumalli LK, McEwan JC, Nazareth LV, Schnabel RD, Weinstock GM, Wheeler DA, Ajmone-Marsan P, Boettcher PJ, Caetano AR, Garcia JF, Hanotte O, Mariani P, Skow LC, Sonstegard TS, Williams JL, Diallo B, Hailemariam L, Martinez ML, Morris CA, Silva LO, Spelman RJ, Mulatu W, Zhao K, Abbey CA, Agaba M, Araujo FR, Bunch RJ, Burton J, Gorni C, Olivier H, Harrison BE, Luff B, Machado MA, Mwakaya J, Plastow G, Sim W, Smith T, Thomas MB, Valentini A, Williams P, Womack J, Woolliams JA, Liu Y, Qin X, Worley KC, Gao C, Jiang H, Moore SS, Ren Y, Song XZ, Bustamante CD, Hernandez RD, Muzny DM, Patil S, San Lucas A, Fu Q, Kent MP, Vega R, Matukumalli A, McWilliam S, Sclep G, Bryc K, Choi J, Gao H, Grefenstette JJ, Murdoch B, Stella A, Villa-Angulo R, Wright M, Aerts J, Jann O, Negrini R, Goddard ME, Hayes BJ, Bradley DG, Barbosa da Silva M, Lau LP, Liu GE, Lynn DJ, Panzitta F, Dodds KG, Bovine HapMap Consortium (2009). Genome-wide survey of SNP variation uncovers the genetic structure of cattle breeds. Science. 324(5926):528.
36. Hoyt AM (1982). History of Texas Longhorns. Texas Longhorn Journal. 1–48.
37. McTavish EJ, Decker JE, Schnabel RD, Taylor JF, Hillis DM (2013). New World cattle show ancestry from multiple independent domestication events. PNAS. 110(15):E1398-E406.
38. Mirol PM, Giovambattista G, Liron JP, Dulout FN (2003). African and European mitochondrial haplotypes in South American Creole cattle. Heredity. 91(3):248-54.
39. Barragy TJ (2003). Gathering texas gold. Cayo del Grullo, TX: Cayo Del Grullo Press.
40. Aron DN, Crowe DT (1985). Upper airway obstruction general principles and selected conditions in the dog and cat. Vet Clin North Am Small Anim Pract. 15(5):891-917.
41. Daetwyler HD, Capitan A, Pausch H, Stothard P, van Binsbergen R, Brondum RF, Liao X, Djari A, Rodriguez SC, Grohs C, Esquerre D, Bouchez O, Rossignol M-N, Klopp C, Rocha D, Fritz S, Eggen A, Bowman PJ, Coote D, Chamberlain AJ, Anderson C, VanTassell CP, Hulsegge I, Goddard ME, Guldbrandtsen B, Lund MS, Veerkamp RF, Boichard DA, Fries R, Hayes B (2014). Whole-genome sequencing of 234 bulls facilitates mapping of monogenic and complex traits in cattle. Nat Genet. 46(8):858-65.
42. Gibson E (1915). Some notes on the

Niata breed of cattle (*Bos taurus*). Proc Zool Soc Lond. 85(2):273-7.

43. Yaro M, Munyard KA, Stear MJ, Groth DM (2016). Molecular identification of livestock breeds: a tool for modern conservation biology. Biol Rev. 92(2):993-1010.
44. von den Driesch A (1976). Das Vermessen von Tierknochen aus vor- und frühgeschichtlichen Siedlungen. München: Institut für Paläoanatomie, Domestikationsforschung und Geschichte der Tiermedizin der Universität München.
45. Budras KD, Habel RE, Jahrmärker G, Richter R, Starke D (2003). Bovine Anatomy. Hannover: Schlütersche Verlagsgesellschaft mbH & Company KG.
46. O'Higgins P, Jones N (1998). Facial growth in *Cercocebus torquatus*: an application of three-dimensional geometric morphometric techniques to the study of morphological variation. J Anat. 193(2):251-72.
47. Scott KM (1983). Prediction of body weight of fossil Artiodactyla. Zool J Linn Soc. 77(3):199-215.
48. Anderson JF, Hall-Martin A, Russell DA (1985). Long-bone circumference and weight in mammals, birds and dinosaurs. J Zool. 207(1):53-61.
49. Janis CM (1990). Correlation of cranial and dental variables with body size in ungulates and macropodoids. In: Damuth JD, MacFadden BJ, editors. Body Size in Mammalian Paleobiology: Estimation and Biological Implications. Cambridge: Cambridge University Press; p. 255-99.
50. Bookstein FL (1991). Morphometric tools for landmark data. Geometry and Biology. Cambridge: Cambridge University Press.
51. Mitteroecker P, Gunz P (2009). Advances in geometric morphometrics. Evol Biol. 36(2):235-47.
52. Adams DC, Rohlf FJ, Slice DE (2004). Geometric morphometrics: Ten years of progress following the 'revolution'. Ital J Zool. 71(1):5-16.
53. Adams DC, Otárola-Castillo E (2013). geomorph: an R package for the collection and analysis of geometric morphometric shape data. Methods Ecol Evol. 4(4):393–399.
54. R Development Core Team (2015). R: A language and environment for statistical computing. Version 3.2.3. http://www.R-project.org
55. Zelditch ML, Swiderski DL, Sheets HD (2012). Geometric morphometrics for biologists - a primer. 2nd edition. San Diego: Academic Press.
56. Mendoza M, Janis CM, Palmqvist P (2006). Estimating the body mass of extinct ungulates: a study on the use of multiple regression. J Zool. 270(1):90-101.
57. Thomason JJ (1991). Cranial strength in relation to estimated biting forces in some mammals. Can J Zool. 69(9):2326-33.
58. Wroe S, McHenry C, Thomason J (2005). Bite club: comparative bite force in big biting mammals and the prediction of predatory behaviour in fossil taxa. Proc Biol Sci. 272(1563):619-25.
59. Turnbull WD (1970). Mammalian masticatory apparatus. Fieldiana Geol. 18(2):147-356.
60. Attard MRG, Wilson LAB, Worthy TH, Scofield P, Johnston P, Parr WCH, Wroe S (2016). Moa diet fits the bill: virtual reconstruction incorporating mummified remains and prediction of biomechanical performance in avian giants. Proc Biol Sci. 283(1822): 2015-43.
61. Attard MRG, Parr WCH, Wilson LAB, Archer M, Hand SJ, Rogers TL, Wroe S (2014). Virtual reconstruction and prey size preference in the mid cenozoic thylacinid, *Nimbacinus dicksoni* (Thylacinidae, Marsupialia). PLoS ONE. 9(4):e93088.
62. Wroe S, Chamoli U, Parr WCH, Clausen P, Ridgely R, Witmer L (2013). Comparative biomechanical modeling of metatherian

and placental saber-tooths: a different kind of bite for an extreme pouched predator. PLoS ONE. 8(6):e66888.

63. Wroe S, Ferrara TL, McHenry CR, Curnoe D, Chamoli U (2010). The craniomandibular mechanics of being human. Proc Biol Sci. 277:3579-86.

64. Strait DS, Wang Q, Dechow PC, Ross CF, Richmond BG, Spencer MA, Patel BA (2005). Modeling elastic properties in finite-element analysis: how much precision is needed to produce an accurate model? Anat Rec A Discov Mol Cell Evol Biol. 283A(2):275-87.

65. Smith AL, Benazzi S, Ledogar JA, Tamvada K, Pryor Smith LC, Weber GW, Spencer MA, Lucas PW, Michael S, Shekeban A, Al-Fadhalah K, Almusallam AS, Dechow PC, Grosse IR, Ross CF, Madden RH, Richmond BG, Wright BW, Wang Q, Byron C, Slice DE, Wood S, Dzialo C, Berthaume MA, Casteren A, Strait DS (2015). The feeding biomechanics and dietary ecology of *Paranthropus boisei.* Anat Rec. 298(1):145-67.

66. McHenry CR, Clausen PD, Daniel WJT, Meers MB, Pendharkar A (2006). Biomechanics of the rostrum in crocodilians: A comparative analysis using finite-element modeling. Anat Rec A Discov Mol Cell Evol Biol. 288A(8):827-49.

67. Nalla RK, Kinney JH, Ritchie RO (2003). Mechanistic fracture criteria for the failure of human cortical bone. Nat Mater. 2(3):164-8.

68. Keyak JH, Rossi SA (2000). Prediction of femoral fracture load using finite element models: an examination of stress- and strain-based failure theories. J Biomech. 33(2):209-14.

69. Krüttli A, Bouwman A, Akgül G, Della Casa P, Rühli F, Warinner C (2014). Ancient DNA analysis reveals high frequency of european lactase persistence allele (T-13910) in medieval Central Europe. PLoS ONE. 9(1):e86251.

70. Pickrell JK, Pritchard JK (2012). Inference of population splits and mixtures from genome-wide allele frequency data. PLoS Genet. 8(11):e1002967.

Supplementary Information

‘Resurrecting’ Darwin’s Niata - anatomical, biomechanical, genetic, and morphometric studies of morphological novelty in cattle

Supplementary Table 1: Measurements of all examined Niata skulls.

Skull						
von den Driesch 1976 (sin/dex averaged)		MLP 1126	MLP 1556	MLP 1465	ZMB_ Mam_105902	MNHN 1933-122
1	total length	39.6	36.9	32.6	34.4	37
2	condylobasal length	38.6	37.5	33	34	36
3	basal length	34.3	34.8	30.7	31.7	33
4	small skull length	27.5	27.6	23.4	25.6	-
5	premolar - prosthion	11.7	10.6	9.7	9.4	-
6	neurocranial length	25	23.1	24	20.5	-
7	viscerocranial length	19.2	17.5	13.9	14.9	17.4
8	median frontal length	20	18.5	16.8	18.1	18.5
9	biggest frontal length	20.5	23	20.4	21.7	22.8
10	small upper skull length	28.8	27.2	24.9	26.5	27.3
11	akrokranion - Infraorbital	29.5	30	25.2	28.1	-
12	biggest nasal length	9.1	8.8	7.8	8.6	8.6
13	posterior margin of condylus occipitale - entorbitale	23	22.9	18.2	18.7	-
14	lateral face length	23.9	24.5	21	21.4	22.7
15	posterior margin of condylus occipitale - infraorbitale	28.5	28.8	23	25.6	-
16	infraorbitale - prosthion	12.5	17.3	10.3	10.5	-
17	prosthion - posterior margin of M3	23.3	23.4	20.7	17.6	21.3
18	prosthion - anterior margin of palate bone from ventral	16.8	15.2	14	14	14.9
19	premaxillary length	12.2	11	11.4	10.7	12.3
20	length tooth row	11.4	12.4	10.4	11.4	-
21	length molar row	7.5	8.1	7.1	6.8	8.7
22	length premolar row	5.3	5.3	4.6	6.4	-
23	length orbita	5.4	6.5	5.4	5.8	5.8
24	width orbita	6.4	6.7	5.6	6.9	6.6
25	mastoid width	25.5	23.5	17.2	20.7	24.3
26	width between occipital condyli	11.4	10.8	8.8	10.4	9.6

27	width between the bases of the processi jugulare	17.5	17.4	12.4	16	-
28	width foramen magnum	4.3	3.6	3.5	3.1	3.2
29	height foramen magnum	4.5	4	3.4	4.3	3.7
30	parietal width	18.5	16.8	11.1	13.5	14.8
31	width between bases of the horns	19.5	22.1	15.9	22.2	16.5
32	smallest frontal width	21.3	20.9	15.2	19	20
33	biggest frontal width between orbits	24	24	19.1	21	23.2
34	smallest frontal width between orbits	17.5	17	14.2	15	17.6
35	cheek width	19.5	18.5	16.3	15.3	-
36	nasal width	-	7	5.6	6.1	7.6
37	width of os incisivi	8.9	8.7	7.5	7	8.2
38	biggest width between lateral margins of alveola	15.2	14.2	13	12.2	-
39	height fossa temporalis	3.7	4	3.3	4.5	4.5
40	biggest height of occipital	17.5	18.5	13.9	15.3	16.4
41	smallest height of occipital	13.3	14.9	10.6	12.3	12.7
42	width between tips of the horns (without curvature)	60.5	69	54.2	59	79.2
	length P2	1.8	1.6	-	-	-
	width P2	1.6	1.3	-	-	-
	length P3	1.9	1.8	-	-	-
	width P3	1.6	1.5	-	-	-
	length P4	1.9	1.8	1.7	-	-
	width P4	1.9	1.7	1.9	-	-
	length M1	2	2.5	2.1	2.8	2.3
	width M1	2.1	2	2	1.9	1.9
	length M2	2.6	2.9	2.5	3	2.9
	width M2	2.2	1.9	2.3	1.7	1.9
	length M3	3	2.9	2.8	-	2.6
	width M3	2.3	1.6	1.9	-	1.7
Mandible						
1	length mandible (gonion caudale - infradentale)	34.7	34.3	30	30	-
2	length mandible (posterior margin of processus condyloideus - infradentale)	32.9	32.3	29	29.6	-
3	width ascending ramus	11.4	10.7	9	9.4	-
4	length body of mandible	23.3	23.2	21.1	22	-
5	gonion caudale - anterior alveola p2	24.7	25	21.5	22.9	-
6	gonion caudale - foramen mentale	28.4	28.4	25.7	26.6	-
7	length tooth row	13.7	14.4	12.8	13.7	-
8	length molar row	9.3	9.4	8.5	8.4	-

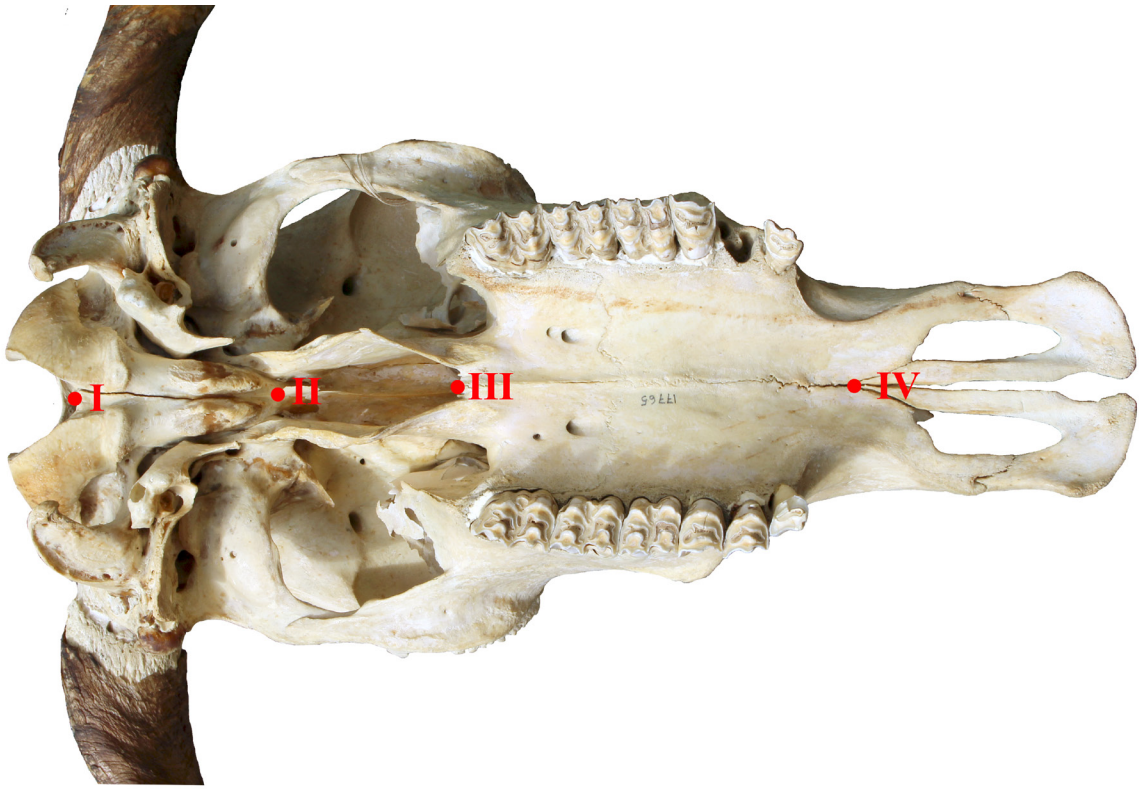
9	length premolar row	5.1	5.5	4.8	5.8	-
11	length diastema	8.6	8	7.5	7.5	-
12	gonion ventrale - tip processus condyloideus	17.7	16.4	15.6	14	-
13	gonion ventrale - ventralmost tip of incisura mandibulae	15.5	15	14	13.5	-
14	length ascending ramus	23	21.1	20.2	19.8	-
15a	height mandible posterior to m3	8.1	7.7	6.1	6.9	-
15b	height mandible between p4 and m1	5.3	5.4	4.3	4.9	-
15c	height mandible anterior to p2	4.1	3.8	3.3	3.6	-
	length p2	1	1.1	-	-	-
	width p2	0.9	0.9	-	-	-
	length p3	1.8	1.9	-	-	-
	width p3	1.1	1	-	-	-
	length p4	2.2	2.2	2.1	2.9	-
	width p4	1.2	1.2	1.2	1.2	-
	length m1	2.2	2.5	2.2	2.7	-
	width m1	1.4	1.2	1.2	1.3	-
	length m2	2.6	2.8	2.5	2.4	-
	width m2	1.5	1.2	1.3	1.2	-
10	length m3	4	3.5	3.7	-	-
10	width m3	1.6	1.3	1.3	-	-

Material

The cranial and postcranial material examined in this study is housed in following institutions: Institut für Haustierkunde (former; now Zoologisches Institut, Populationsgenetik), Christian-Albrechts-Universität zu Kiel, Germany (IfH), Naturhistorisches Museum Basel (NMB), Archäologisch Zoologische Sammlung des Naturhistorischen Museums Wien (NHM), Natural History Museum of Denmark, University of Copenhagen (SNM-KU), Muséum National d'Histoire Naturelle Paris (MNHN), Museum für Naturkunde Berlin (MfN), Museo de la Plata (MLP), Paleontological Institute and Museum University of Zurich (PIMUZ), Zentralmagazin Naturwissenschaftlicher Sammlungen – Museum für Haustierkunde „Julius Kühn" – der Martin-Luther-Universität Halle-Wittenberg (ZNS Haustierkunde), and Zoological Museum University of Zurich (ZMUZH).

The basicranial angle

The basicranial angle or prebasial angle describes the relationship between the base of the viscerocranium and neurocranium. This angle is divided into three different types: lower as 180° are called klinorhynch, higher ones are called airorhynch, and an angle of 180° is called orthocranial. It was assumed that originally all skulls were orthocranial [1, 2]. During domestication, the basicranial angle can change substantially, as is the case for domesticated dogs were a range from 158° to 183° was described [3, 4]. This range is higher in cattle ranging from 158° to 193°. Incidentally, the data shows a gradual change from the aurochs to Niata. In pigs, it was suggested that aiorhynchie has an evolutionary advantage for feeding. The diet of wild boar and domesticated pigs differs and airorhynchie might facilitate a more optimal placement of the lower jaw for the different diet humans provided [2]. We used 4 landmarks to obtain basicranial angles as shown and defined in Supplementary Figure 1 and Supplementary Table 2.



Supplementary Figure 1: Landmarks used to measure the basicranial angle. I: ven-tral-medial edge of foramen magnum, II: suture between presphenoid and vomer in midline, III: posterior-medial tip of the horizontal plate of the palatine bone, IV: ventral suture between premaxillary and maxillary bone in midline

Supplementary Table 2: Basicranial angle of examined cattle breeds.

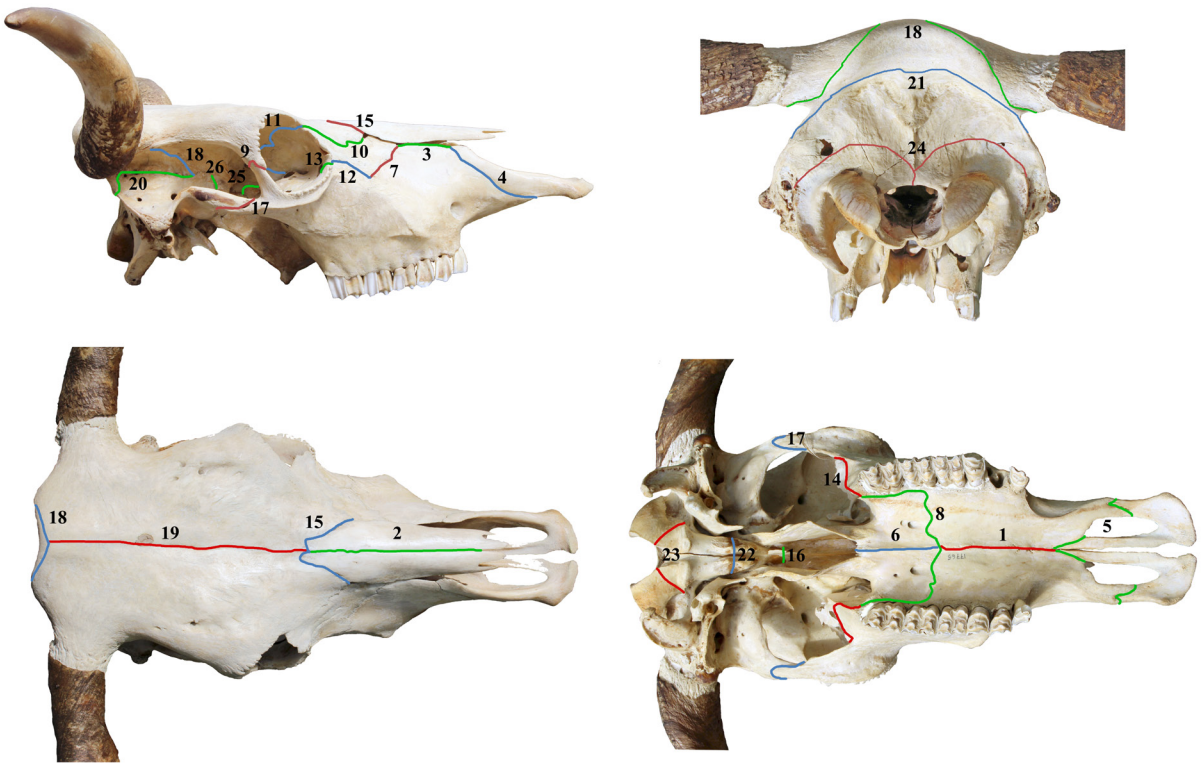
Breed (n: 36)	Average Angle	StDev	n	Dorso-Basal Curvature
Abessinian	173	-	1	klinorhynchy
Andalusian	165	-	1	klinorhynchy
Angeln	169	0	2	klinorhynchy
Bos primigenius (Aurochs)	158	1.71	4	klinorhynchy
Brazilian	171	6.24	3	klinorhynchy
Cretan	166	2.83	2	klinorhynchy
Danish Red	174	-	1	klinorhynchy
Dexter	179	-	1	klinorhynchy
Galloway	172	-	1	klinorhynchy
German Black Pied	169	-	1	klinorhynchy
Graubündner (Swiss Brown)	171	-	1	klinorhynchy
Guernsey	168	-	1	klinorhynchy
Hinterwälder	169	-	1	klinorhynchy
Iceland	170	0	2	klinorhynchy
Jamtland	169	3.21	5	klinorhynchy
Japanese	167	-	1	klinorhynchy
Jersey	178	3.64	8	klinorhynchy
Jutland	165	2.12	2	klinorhynchy
Kerry	172	-	1	klinorhynchy
Limousin	167	-	1	klinorhynchy
Longhorn (British)	172	-	1	klinorhynchy
Niata	193	10.61	2	airorhynchy
Red Poll	170	-	1	klinorhynchy
Sanga	160	-	1	klinorhynchy
Sardinian	165	4.24	2	klinorhynchy
Schwyz (Swiss Brown)	170	3.54	2	klinorhynchy
Scottish Highland	168	-	1	klinorhynchy
Shorthorn (British)	169	2.08	3	klinorhynchy
Sicilian	179	-	1	klinorhynchy
Småland	171	7.78	2	klinorhynchy
Spanish Fighting	166	1.99	7	klinorhynchy
Swedish Mountain	170	-	1	klinorhynchy
Watussi	169	2.83	2	klinorhynchy
White Park	169	1.41	2	klinorhynchy
Wilstermarsch (German Red Pied)	168	-	1	klinorhynchy
Zebu	164	6.32	9	klinorhynchy

References

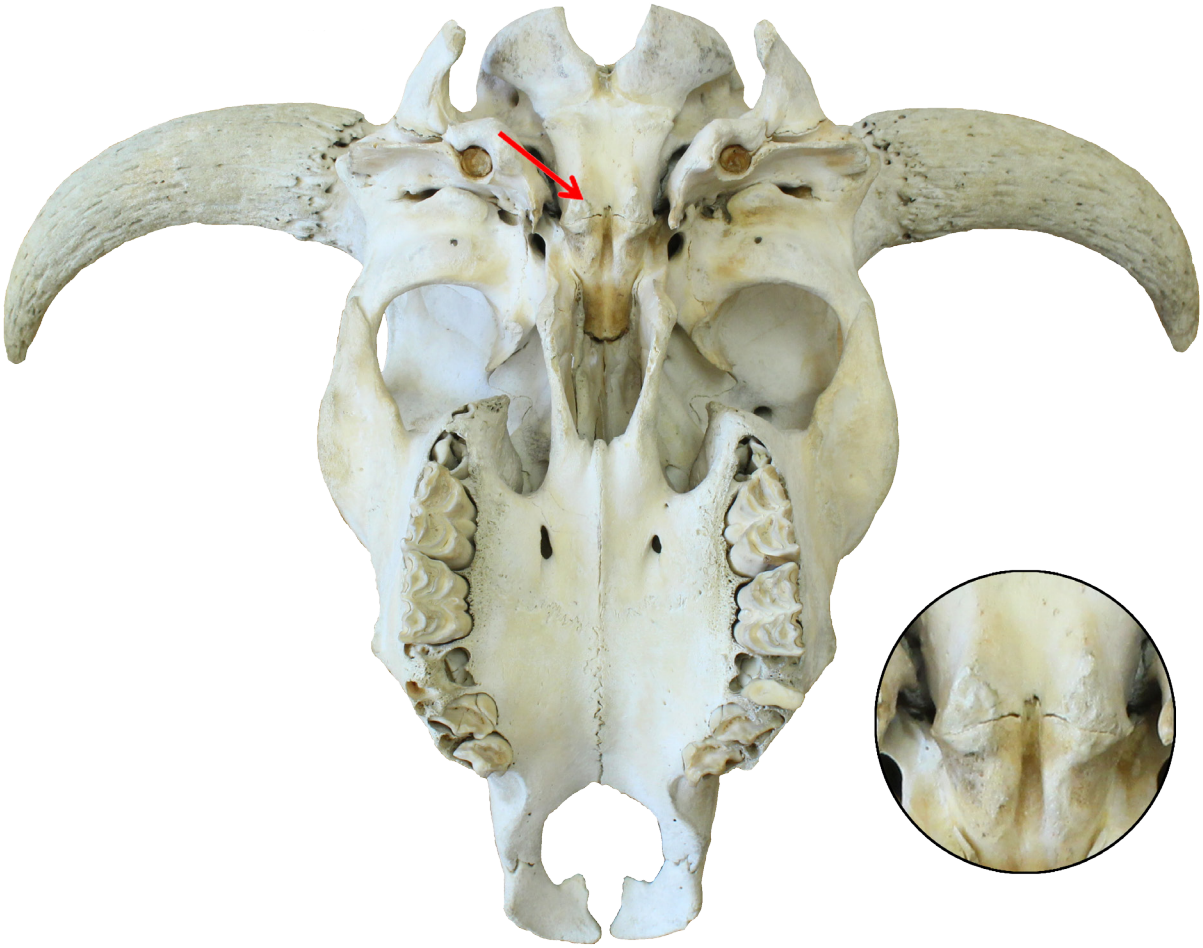
1. Hofer H (1952). Der Gestaltwandel des Schädels der Säugetiere und Vögel, mit besonderer Berücksichtigung der Knickungstypen und der Schädelbasis. Verh Anat Ges. 50:102-13.
2. Thenius E (1970). Zum Problem der Airorhynchie des Säugetierschädels – Ein Deutungsversuch. Zool Anz. 185(3/4):159-72.
3. Geiger M, Haussman S (2016). Cranial suture closure in domestic dog breeds and its relationships to skull morphology. Anat Rec. 299(4):412-20.
4. Nussbaumer M (1982). On the variability of dorso-basal curvatures in skulls of domestic dogs. Zool Anz. 209(1-2):1-32.

External suture obliteration pattern

We investigated the obliteration of 26 sutures externally to assess first if there are overall changes in the obliteration pattern between Niata cattle and other breeds and second if changes relating to chondrodysplasia can be detected (Supplementary Figure 2, Supplementary Table 3). Suture obliteration is correlated with changes in skull shape. Dogs with airorhynch skulls exhibit significant higher closure scores than their klinorhynch counterparts and both differ significantly from the wolf [1]. In cattle only the Niata was airorhynch all other cattle breeds were klinorhynch. Suture obliteration pattern was not different in Niata cattle. The rarity of juvenile Niata skulls, however, does limit hypotheses on similarity or differences in the overall obliteration scores. One suture was of greater informative value as early fusion of the basioccipital-basisphenoid suture is indicative for chondrodysplasia in cattle [2]. The skull ZMB_Mam_105902 can be dated to an individual age of 24-30 months based on tooth eruption [3] and exhibits an open suture at this bone contact area (Supplementary Figure 3).



Supplementary Figure 2: Sutures used to assess the external suture obliteration pattern during growth of Niata and other cattle. Corresponding suture description to numbers are found in Supplementary Table 3.



Supplementary Figure 3: Ventral view of Niata skull ZMB_Mam_105902. Note the open suture between basioccipital and basisphenoid bone and the eruption of the premolars as well as third molar indicating and age of 24 – 30 months [3].

Supplementary Table 3: External suture obliteration in Niata as well as other cattle breeds and corresponding relative suture closure score.

	Breed	Danish Red	Danish Red	x	x
	Inventory Number	SNM-KU MK 496	SNM-KU MK 497	SNM-KU Nov. 1935	SNM-KU 14/1-1910
	Age in months	0.23	2	8	9
	Sex	Male	Male	Male	Male
1	Intermaxillary	0	0	0	0
2	Internasal	0	0	0	0
3	Nasal-Maxillary	0	0	0	0
4	Premaxillary-Maxillary (f)	0	0	0	0
5	Premaxillary-Maxillary (v)	0	0	0	0
6	Interpalatine	0	0	0	0
7	Maxillary-Lacrimal (f)	0	0	0	0
8	Maxillary-Palatine (v)	0	0	0	0
9	Jugal-Frontal	0	0	0	0
10	Lacrimal-Frontal (f)	0	0	0	0
11	Lacrimal-Frontal (o)	0	0	0	0
12	Lacrimal-Jugal (f)	0	0	0	0
13	Lacrimal-Jugal (o)	0	0	0	0
14	Maxillary-Lacrimal (o)	0	0	0	0
15	Nasal-Frontal	0	0	0	0
16	Basisphenoid - Presphenoid	0	0	0	0
17	Jugal-Squamosal	0	0	0	0
18	Frontal-Parietal	0	0	1	0
19	Interfrontal	0	0	0	0
20	Parietal-Squamosal	0	0	0	0
21	Supraoccipital-Parietal	0	1	2	2
22	Basisphenoid-Basioccipital	0	0	0	0
23	Exoccipital-Basioccipital	0	0	0	1
24	Exoccipital-Supraoccipital	0	0	0	0
25	Orbitosphenoid-Frontal	0	0	0	0
26	Alisphenoid-Squamosal	0	0	0	0
	Suture Closure Score	0.00	0.04	0.12	0.12
	Breed	German Black Pied	German Black Pied	German Black Pied	German Black Pied
	Inventory Number	IfH 11316	IfH 11318	IfH 11319	IfH 11315
	Age in months	10	10	10	10
	Sex	Female	Female	Female	Female
1	Intermaxillary	0	0	0	0
2	Internasal	0	0	0	0
3	Nasal-Maxillary	0	0	0	0
4	Premaxillary-Maxillary (f)	0	0	0	0
5	Premaxillary-Maxillary (v)	0	0	0	0
6	Interpalatine	0	0	0	0

7	Maxillary-Lacrimal (f)	0	0	0	0
8	Maxillary-Palatine (v)	0	0	0	0
9	Jugal-Frontal	0	0	0	0
10	Lacrimal-Frontal (f)	0	0	0	0
11	Lacrimal-Frontal (o)	0	0	0	0
12	Lacrimal-Jugal (f)	0	0	0	0
13	Lacrimal-Jugal (o)	0	0	0	0
14	Maxillary-Lacrimal (o)	0	0	0	0
15	Nasal-Frontal	0	0	0	0
16	Basisphenoid - Presphenoid	0	0	0	0
17	Jugal-Squamosal	0	0	0	0
18	Frontal-Parietal	0	0	0	0
19	Interfrontal	0	0	0	0
20	Parietal-Squamosal	0	0	0	0
21	Supraoccipital-Parietal	2	2	2	2
22	Basisphenoid-Basioccipital	0	0	0	0
23	Exoccipital-Basioccipital	0	0	0	0
24	Exoccipital-Supraoccipital	0	0	0	0
25	Orbitosphenoid-Frontal	0	0	0	0
26	Alisphenoid-Squamosal	0	0	0	0
	Suture Closure Score	0.08	0.08	0.08	0.08
	Breed	German Black Pied	x	German Black Pied	German Black Pied
	Inventory Number	IfH 11317	SNM-KU MK 168	IfH 11361	IfH 11283
	Age in months	10	12	12.5	15
	Sex	Female	Male	Female	Female
1	Intermaxillary	0	0	0	0
2	Internasal	0	0	0	0
3	Nasal-Maxillary	0	0	0	0
4	Premaxillary-Maxillary (f)	0	0	0	0
5	Premaxillary-Maxillary (v)	0	0	0	0
6	Interpalatine	0	0	0	0
7	Maxillary-Lacrimal (f)	0	0	0	0
8	Maxillary-Palatine (v)	0	0	0	0
9	Jugal-Frontal	0	0	0	0
10	Lacrimal-Frontal (f)	0	0	0	0
11	Lacrimal-Frontal (o)	0	0	0	0
12	Lacrimal-Jugal (f)	0	0	0	0
13	Lacrimal-Jugal (o)	0	0	0	0
14	Maxillary-Lacrimal (o)	0	0	0	0
15	Nasal-Frontal	0	0	0	0
16	Basisphenoid - Presphenoid	0	0	0	0
17	Jugal-Squamosal	0	0	0	0
18	Frontal-Parietal	0	1	0	0
19	Interfrontal	0	0	0	0
20	Parietal-Squamosal	0	0	0	0
21	Supraoccipital-Parietal	2	2	2	2

22	Basisphenoid-Basioccipital	0	0	0	0
23	Exoccipital-Basioccipital	1	2	0	2
24	Exoccipital-Supraoccipital	0	0	0	0
25	Orbitosphenoid-Frontal	0	0	0	0
26	Alisphenoid-Squamosal	0	0	0	0
	Suture Closure Score	0.12	0.19	0.08	0.15
	Breed	x	x	x	x
	Inventory Number	SNM-KU MK 171	SNM-KU MK 175	IfH 11320	SNM-KU MK 164
	Age in months	15	15	15	16
	Sex	Male	Male	Female	Male
1	Intermaxillary	0	0	0	0
2	Internasal	0	0	0	0
3	Nasal-Maxillary	0	0	0	0
4	Premaxillary-Maxillary (f)	0	0	0	0
5	Premaxillary-Maxillary (v)	0	0	0	0
6	Interpalatine	0	0	0	0
7	Maxillary-Lacrimal (f)	0	0	0	0
8	Maxillary-Palatine (v)	0	0	0	0
9	Jugal-Frontal	0	0	0	0
10	Lacrimal-Frontal (f)	0	0	0	0
11	Lacrimal-Frontal (o)	0	0	0	0
12	Lacrimal-Jugal (f)	0	0	0	0
13	Lacrimal-Jugal (o)	0	0	0	0
14	Maxillary-Lacrimal (o)	0	0	0	0
15	Nasal-Frontal	0	0	0	0
16	Basisphenoid - Presphenoid	0	0	0	0
17	Jugal-Squamosal	0	0	0	0
18	Frontal-Parietal	0	1	0	1
19	Interfrontal	0	0	0	0
20	Parietal-Squamosal	0	0	0	0
21	Supraoccipital-Parietal	2	2	2	2
22	Basisphenoid-Basioccipital	0	0	0	0
23	Exoccipital-Basioccipital	1	2	2	2
24	Exoccipital-Supraoccipital	0	0	0	0
25	Orbitosphenoid-Frontal	0	0	0	0
26	Alisphenoid-Squamosal	0	0	0	0
	Suture Closure Score	0.12	0.19	0.15	0.19
	Breed	x	Hinterwälder	x	Scottish Highland
	Inventory Number	IfH 11363	IfH 4624	SNM-KU MK 162	SNM-KU MK 571
	Age in months	16.5	16.5	21	24
	Sex	Female	Male	Male	Male
1	Intermaxillary	0	0	0	0
2	Internasal	0	0	0	0
3	Nasal-Maxillary	0	0	0	0
4	Premaxillary-Maxillary (f)	0	0	0	0
5	Premaxillary-Maxillary (v)	0	0	0	0

6	Interpalatine	0	0	0	0
7	Maxillary-Lacrimal (f)	0	0	0	0
8	Maxillary-Palatine (v)	0	0	0	0
9	Jugal-Frontal	0	0	0	0
10	Lacrimal-Frontal (f)	0	0	0	0
11	Lacrimal-Frontal (o)	0	0	0	0
12	Lacrimal-Jugal (f)	0	0	0	0
13	Lacrimal-Jugal (o)	0	0	0	0
14	Maxillary-Lacrimal (o)	0	0	0	0
15	Nasal-Frontal	0	0	0	0
16	Basisphenoid - Presphenoid	0	0	0	0
17	Jugal-Squamosal	0	0	0	0
18	Frontal-Parietal	0	1	1	1
19	Interfrontal	0	0	0	1
20	Parietal-Squamosal	0	0	0	0
21	Supraoccipital-Parietal	2	2	2	2
22	Basisphenoid-Basioccipital	0	0	0	1
23	Exoccipital-Basioccipital	2	2	2	2
24	Exoccipital-Supraoccipital	0	0	0	1
25	Orbitosphenoid-Frontal	0	0	0	1
26	Alisphenoid-Squamosal	0	0	0	0
	Suture Closure Score	0.15	0.19	0.19	0.35
	Breed	Niata	German Black Pied	x	Longhorn (British)
	Inventory Number	ZMB_Mam_105902	IfH 11522	IfH 4185	ZNS Haustierkunde B lgh 4
	Age in months	24	27.5	28	28
	Sex	x	x	Female	Male
1	Intermaxillary	0	0	0	0
2	Internasal	0	0	0	0
3	Nasal-Maxillary	0	0	0	0
4	Premaxillary-Maxillary (f)	0	0	0	0
5	Premaxillary-Maxillary (v)	0	0	0	0
6	Interpalatine	0	0	0	0
7	Maxillary-Lacrimal (f)	0	0	0	0
8	Maxillary-Palatine (v)	0	0	0	0
9	Jugal-Frontal	0	0	0	0
10	Lacrimal-Frontal (f)	0	0	0	0
11	Lacrimal-Frontal (o)	0	0	0	0
12	Lacrimal-Jugal (f)	0	0	0	0
13	Lacrimal-Jugal (o)	0	0	0	0
14	Maxillary-Lacrimal (o)	0	0	0	0
15	Nasal-Frontal	0	0	0	0
16	Basisphenoid - Presphenoid	0	0	0	0
17	Jugal-Squamosal	0	0	0	0
18	Frontal-Parietal	1	0	1	1
19	Interfrontal	1	0	0	1

20	Parietal-Squamosal	0	0	0	0
21	Supraoccipital-Parietal	2	2	2	2
22	Basisphenoid-Basioccipital	0	0	1	0
23	Exoccipital-Basioccipital	2	2	2	0
24	Exoccipital-Supraoccipital	0	0	1	0
25	Orbitosphenoid-Frontal	0	0	0	0
26	Alisphenoid-Squamosal	0	0	0	0
	Suture Closure Score	0.23	0.15	0.27	0.15
	Breed	Zebu	Zebu	Polled	x
	Inventory Number	IfH 1131	IfH 1130	SNM-KU No. Nmb.	SNM-KU MK 174
	Age in months	30	30	30	30
	Sex	Female	Female	Male	Male
1	Intermaxillary	0	0	0	0
2	Internasal	0	0	0	0
3	Nasal-Maxillary	0	0	0	0
4	Premaxillary-Maxillary (f)	0	0	0	0
5	Premaxillary-Maxillary (v)	0	0	0	0
6	Interpalatine	0	0	0	0
7	Maxillary-Lacrimal (f)	0	0	0	0
8	Maxillary-Palatine (v)	0	0	0	0
9	Jugal-Frontal	0	0	0	0
10	Lacrimal-Frontal (f)	0	0	0	0
11	Lacrimal-Frontal (o)	0	0	0	0
12	Lacrimal-Jugal (f)	0	0	0	0
13	Lacrimal-Jugal (o)	0	0	0	0
14	Maxillary-Lacrimal (o)	0	0	0	0
15	Nasal-Frontal	0	0	0	0
16	Basisphenoid - Presphenoid	0	0	0	0
17	Jugal-Squamosal	0	0	0	0
18	Frontal-Parietal	1	1	0	1
19	Interfrontal	1	1	0	0
20	Parietal-Squamosal	0	0	0	0
21	Supraoccipital-Parietal	2	2	2	2
22	Basisphenoid-Basioccipital	1	1	0	1
23	Exoccipital-Basioccipital	2	2	2	2
24	Exoccipital-Supraoccipital	1	1	0	0
25	Orbitosphenoid-Frontal	0	0	0	0
26	Alisphenoid-Squamosal	0	0	0	0
	Suture Closure Score	0.31	0.31	0.15	0.23
	Breed	Danish Red	Danish Red	Hinterwälder	x
	Inventory Number	SNM-KU 10/4-1957	SNM-KU 7/3 1955	ZNS Haustierkunde B htw 1	IfH 11321
	Age in months	33	36	36	37
	Sex	Female	Female	Female	Female
1	Intermaxillary	0	0	0	0
2	Internasal	0	0	0	0

3	Nasal-Maxillary	0	0	0	0
4	Premaxillary-Maxillary (f)	0	0	0	0
5	Premaxillary-Maxillary (v)	0	0	0	0
6	Interpalatine	0	0	0	0
7	Maxillary-Lacrimal (f)	0	0	0	0
8	Maxillary-Palatine (v)	0	0	0	0
9	Jugal-Frontal	0	0	0	0
10	Lacrimal-Frontal (f)	0	0	0	0
11	Lacrimal-Frontal (o)	0	0	0	0
12	Lacrimal-Jugal (f)	0	0	0	0
13	Lacrimal-Jugal (o)	0	0	0	0
14	Maxillary-Lacrimal (o)	0	0	0	0
15	Nasal-Frontal	0	0	0	0
16	Basisphenoid - Presphenoid	0	0	1	0
17	Jugal-Squamosal	0	0	0	0
18	Frontal-Parietal	1	1	1	1
19	Interfrontal	1	1	1	0
20	Parietal-Squamosal	0	0	0	1
21	Supraoccipital-Parietal	2	2	2	2
22	Basisphenoid-Basioccipital	2	2	2	0
23	Exoccipital-Basioccipital	2	2	2	2
24	Exoccipital-Supraoccipital	2	1	2	1
25	Orbitosphenoid-Frontal	0	0	0	0
26	Alisphenoid-Squamosal	0	0	0	0
	Suture Closure Score	0.38	0.35	0.42	0.27
	Breed	Scottish Highland	Niata	Zebu	Spanish Fighting
	Inventory Number	SNM-KU MK 572	MLP 1556	SNM-KU CN 319	SNM-KU CN 2812
	Age in months	42	48	48	48
	Sex	Male	Female	Male	Male
1	Intermaxillary	0	0	0	0
2	Internasal	0	1	1	1
3	Nasal-Maxillary	0	0	0	0
4	Premaxillary-Maxillary (f)	0	0	0	0
5	Premaxillary-Maxillary (v)	0	0	0	0
6	Interpalatine	0	0	0	0
7	Maxillary-Lacrimal (f)	0	0	0	0
8	Maxillary-Palatine (v)	0	0	0	0
9	Jugal-Frontal	0	0	0	0
10	Lacrimal-Frontal (f)	0	0	0	0
11	Lacrimal-Frontal (o)	0	0	0	0
12	Lacrimal-Jugal (f)	0	0	0	0
13	Lacrimal-Jugal (o)	0	0	0	0
14	Maxillary-Lacrimal (o)	0	0	0	0
15	Nasal-Frontal	0	0	0	0
16	Basisphenoid - Presphenoid	0	0	0	0
17	Jugal-Squamosal	0	0	0	0

18	Frontal-Parietal	1	1	1	1
19	Interfrontal	1	1	1	1
20	Parietal-Squamosal	0	0	1	1
21	Supraoccipital-Parietal	2	2	2	2
22	Basisphenoid-Basioccipital	2	2	2	2
23	Exoccipital-Basioccipital	2	2	2	2
24	Exoccipital-Supraoccipital	2	1	2	2
25	Orbitosphenoid-Frontal	1	1	1	0
26	Alisphenoid-Squamosal	0	0	0	0
	Suture Closure Score	0.42	0.42	0.50	0.46
	Breed	Spanish Fighting	Svensk Fjeldrace	Schwyz (Swiss Brown)	Shorthorn
	Inventory Number	SNM-KU CN 2815	SNM-KU MK 137	ZNS Haustierkunde B swyz 5	ZNS Haustierkunde B shh 14
	Age in months	60	60	64	72
	Sex	Male	Male	Female	Male
1	Intermaxillary	0	0	0	0
2	Internasal	0	0	0	1
3	Nasal-Maxillary	0	0	0	0
4	Premaxillary-Maxillary (f)	0	0	0	0
5	Premaxillary-Maxillary (v)	0	0	0	0
6	Interpalatine	0	0	0	0
7	Maxillary-Lacrimal (f)	0	0	0	0
8	Maxillary-Palatine (v)	0	0	0	0
9	Jugal-Frontal	1	0	1	1
10	Lacrimal-Frontal (f)	1	0	1	1
11	Lacrimal-Frontal (o)	0	1	1	1
12	Lacrimal-Jugal (f)	1	0	0	2
13	Lacrimal-Jugal (o)	1	1	0	1
14	Maxillary-Lacrimal (o)	0	0	0	0
15	Nasal-Frontal	0	1	0	0
16	Basisphenoid - Presphenoid	0	2	2	1
17	Jugal-Squamosal	0	0	0	0
18	Frontal-Parietal	1	1	1	1
19	Interfrontal	1	1	1	1
20	Parietal-Squamosal	1	1	2	1
21	Supraoccipital-Parietal	2	2	2	2
22	Basisphenoid-Basioccipital	1	2	2	2
23	Exoccipital-Basioccipital	2	2	2	2
24	Exoccipital-Supraoccipital	2	2	2	2
25	Orbitosphenoid-Frontal	1	0	1	1
26	Alisphenoid-Squamosal	1	0	2	1
	Suture Closure Score	0.62	0.62	0.77	0.81
	Breed	Jersey	Niata	Dexter	Red Danish
	Inventory Number	SNM-KU MK 341	MLP 1465	IfH 33421	RDM 14/11-1959
	Age in months	84	72	96	99
	Sex	Male	Female ?	Female	Female

1	Intermaxillary	0	0	0	0
2	Internasal	0	1	0	1
3	Nasal-Maxillary	0	0	0	0
4	Premaxillary-Maxillary (f)	0	0	0	0
5	Premaxillary-Maxillary (v)	0	0	0	0
6	Interpalatine	0	0	0	0
7	Maxillary-Lacrimal (f)	0	0	0	0
8	Maxillary-Palatine (v)	0	0	0	0
9	Jugal-Frontal	0	0	0	1
10	Lacrimal-Frontal (f)	1	0	1	1
11	Lacrimal-Frontal (o)	1	0	0	0
12	Lacrimal-Jugal (f)	0	0	0	0
13	Lacrimal-Jugal (o)	0	0	1	0
14	Maxillary-Lacrimal (o)	0	0	0	0
15	Nasal-Frontal	0	0	0	0
16	Basisphenoid - Presphenoid	2	2	2	2
17	Jugal-Squamosal	0	0	0	0
18	Frontal-Parietal	1	1	1	1
19	Interfrontal	1	1	1	1
20	Parietal-Squamosal	1	1	1	1
21	Supraoccipital-Parietal	2	2	2	2
22	Basisphenoid-Basioccipital	2	2	2	2
23	Exoccipital-Basioccipital	2	2	2	2
24	Exoccipital-Supraoccipital	2	2	2	2
25	Orbitosphenoid-Frontal	1	2	2	1
26	Alisphenoid-Squamosal	1	2	1	2
	Suture Closure Score	0.65	0.69	0.69	0.73
	Breed	Niata	x	x	Angeln
	Inventory Number	MLP 1126	SNM-KU MK 177	SNM-KU MK 176	ZNS Haustierkunde B agl 7
	Age in months	144	120	124	126
	Sex	Male	Male	Female	Female
1	Intermaxillary	0	1	1	0
2	Internasal	2	2	0	0
3	Nasal-Maxillary	0	0	0	0
4	Premaxillary-Maxillary (f)	1	0	0	0
5	Premaxillary-Maxillary (v)	0	1	0	0
6	Interpalatine	1	0	0	0
7	Maxillary-Lacrimal (f)	2	1	0	0
8	Maxillary-Palatine (v)	1	0	0	0
9	Jugal-Frontal	2	2	1	0
10	Lacrimal-Frontal (f)	1	1	1	0
11	Lacrimal-Frontal (o)	2	1	1	0
12	Lacrimal-Jugal (f)	2	2	0	0
13	Lacrimal-Jugal (o)	2	2	0	0
14	Maxillary-Lacrimal (o)	0	0	0	0

15	Nasal-Frontal	2	1	0	0
16	Basisphenoid - Presphenoid	2	2	2	2
17	Jugal-Squamosal	1	1	0	0
18	Frontal-Parietal	2	1	1	1
19	Interfrontal	1	1	1	1
20	Parietal-Squamosal	2	1	2	1
21	Supraoccipital-Parietal	2	2	2	2
22	Basisphenoid-Basioccipital	2	2	2	2
23	Exoccipital-Basioccipital	2	2	2	2
24	Exoccipital-Supraoccipital	2	2	2	2
25	Orbitosphenoid-Frontal	2	2	1	1
26	Alisphenoid-Squamosal	2	1	1	1
	Suture Closure Score	1.46	1.19	0.77	0.58
	Breed	x	Galloway	x	German Black Pied
	Inventory Number	SNM-KU MK 166	ZNS Haustierkunde B glw 3	SNM-KU MK 179	IfH 24769
	Age in months	132	159	174	252
	Sex	Female	Female	Female	Female
1	Intermaxillary	0	0	0	0
2	Internasal	0	0	1	1
3	Nasal-Maxillary	0	0	0	0
4	Premaxillary-Maxillary (f)	0	0	0	0
5	Premaxillary-Maxillary (v)	0	0	0	0
6	Interpalatine	0	0	0	1
7	Maxillary-Lacrimal (f)	0	0	0	0
8	Maxillary-Palatine (v)	0	0	1	1
9	Jugal-Frontal	1	1	1	2
10	Lacrimal-Frontal (f)	1	1	1	1
11	Lacrimal-Frontal (o)	1	1	1	2
12	Lacrimal-Jugal (f)	0	2	1	2
13	Lacrimal-Jugal (o)	1	1	1	1
14	Maxillary-Lacrimal (o)	0	0	0	0
15	Nasal-Frontal	0	0	0	0
16	Basisphenoid - Presphenoid	2	2	2	2
17	Jugal-Squamosal	0	1	1	1
18	Frontal-Parietal	1	1	1	2
19	Interfrontal	1	1	1	1
20	Parietal-Squamosal	1	2	2	2
21	Supraoccipital-Parietal	2	2	2	2
22	Basisphenoid-Basioccipital	2	2	2	2
23	Exoccipital-Basioccipital	2	2	2	2
24	Exoccipital-Supraoccipital	2	2	2	2
25	Orbitosphenoid-Frontal	2	2	2	2
26	Alisphenoid-Squamosal	2	2	2	2
	Suture Closure Score	0.81	0.96	1.00	1.19
	Breed	Jersey	x	x	

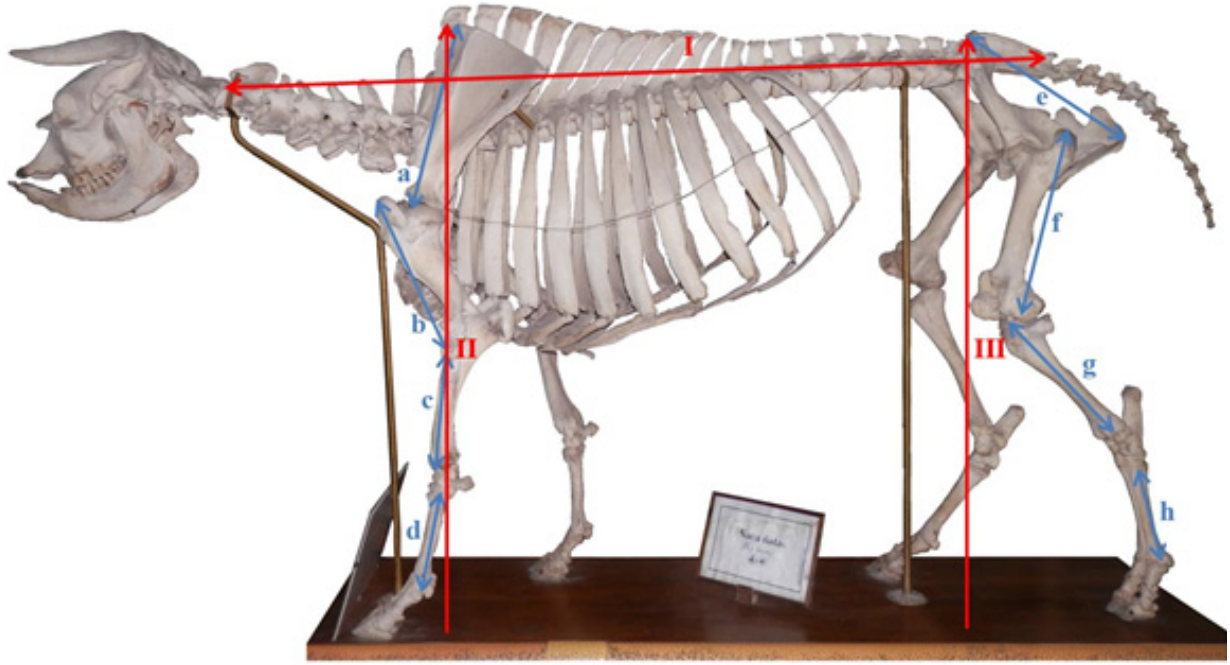
	Inventory Number	IfH 142	SNM-KU MK 161	SNM-KU MK 169
	Age in months	288	318	348
	Sex	Female	Female	Female
1	Intermaxillary	0	0	0
2	Internasal	0	0	1
3	Nasal-Maxillary	0	0	0
4	Premaxillary-Maxillary (f)	0	0	0
5	Premaxillary-Maxillary (v)	0	1	1
6	Interpalatine	0	1	0
7	Maxillary-Lacrimal (f)	0	0	0
8	Maxillary-Palatine (v)	0	1	0
9	Jugal-Frontal	0	1	1
10	Lacrimal-Frontal (f)	1	1	1
11	Lacrimal-Frontal (o)	0	0	0
12	Lacrimal-Jugal (f)	0	1	0
13	Lacrimal-Jugal (o)	0	0	1
14	Maxillary-Lacrimal (o)	0	0	0
15	Nasal-Frontal	0	0	0
16	Basisphenoid - Presphenoid	2	2	2
17	Jugal-Squamosal	1	1	1
18	Frontal-Parietal	1	1	1
19	Interfrontal	1	1	1
20	Parietal-Squamosal	2	1	1
21	Supraoccipital-Parietal	2	2	2
22	Basisphenoid-Basioccipital	2	2	2
23	Exoccipital-Basioccipital	2	2	2
24	Exoccipital-Supraoccipital	2	2	2
25	Orbitosphenoid-Frontal	1	1	1
26	Alisphenoid-Squamosal	2	2	1
	Suture Closure Score	0.73	0.88	0.81

References

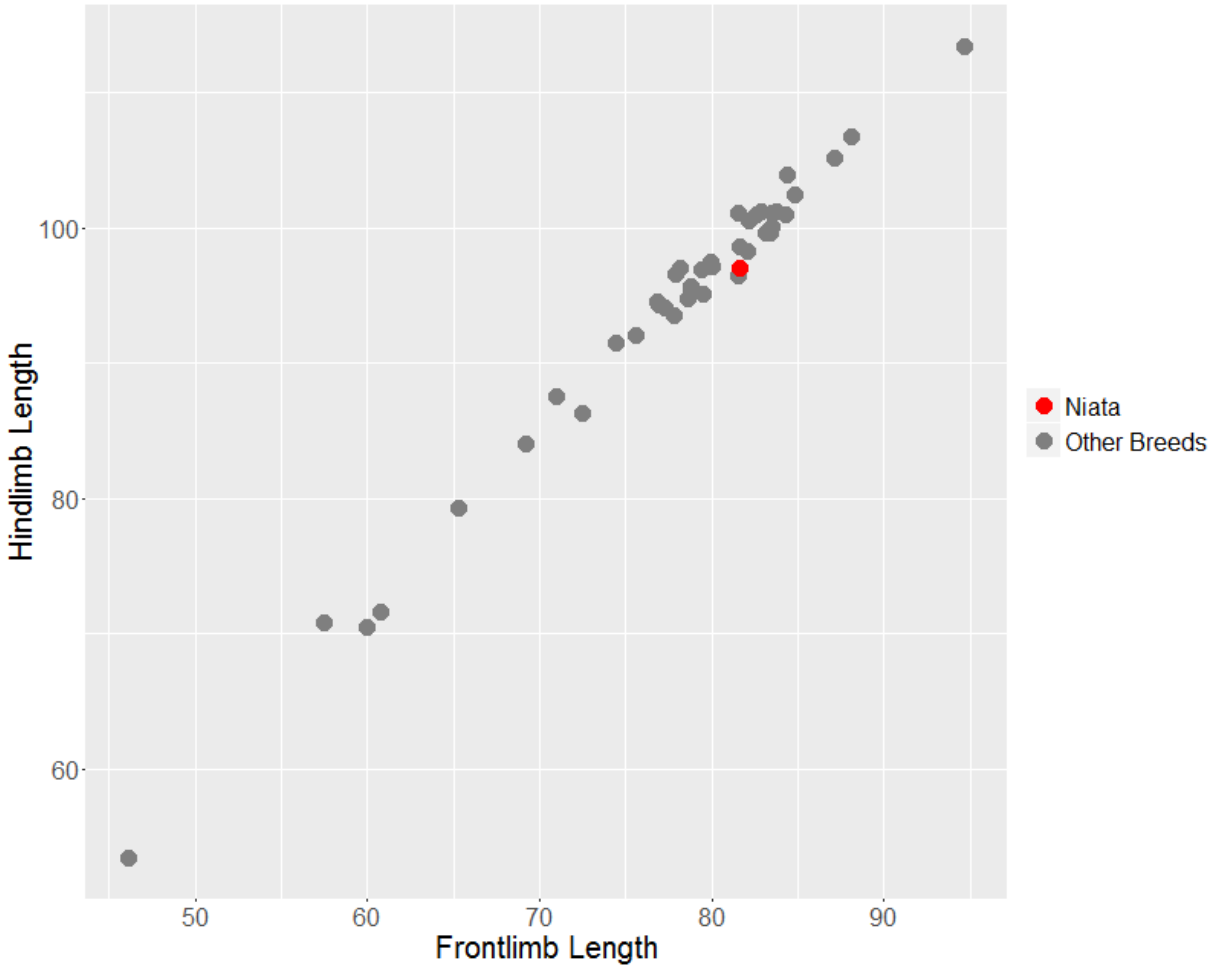
1. Geiger M, Haussman S (2016). Cranial suture closure in domestic dog breeds and its relationships to skull morphology. Anat Rec. 299(4):412-20.
2. McKinley LJ, Steele WT, Hage TJ, Gregory PW (1957). Premature closure of the spheno-occipital synchondrosis in the horned Hereford dwarf of the “short-headed” variety. Am J Anat. 100:269-87.
3. Habermehl K-H (1975). Die Altersbestimmung bei Haus- und Labortieren. 2., vollständig neubearbeitete Auflage. Berlin und Hamburg: Paul Parey.

The size and proportions of the Niata

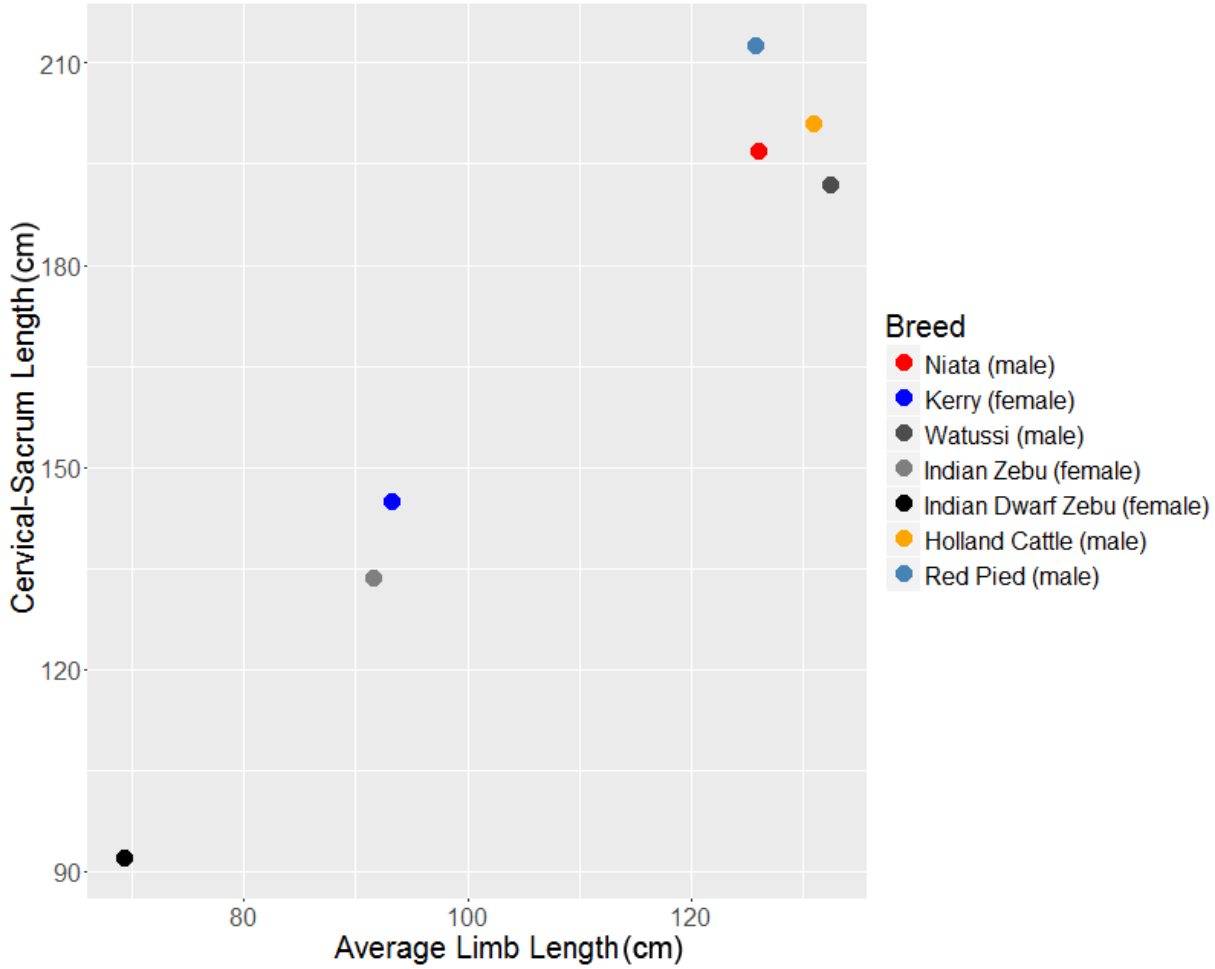
Mutations causing chondrodysplasia are proven to be breed defining in dogs and cattle leading to shortened limbs [1, 2]. A famous example for this in cattle is the Dexter breed from Ireland [1, 3]. The height at the withers of Niata cattle was documented by Baldassare [4]. We used cranial and postcranial measurements to calculate the weight of the Niata to examine (Supplementary Table 4) possible delineations of height to weight in the Niata, which could indicate shortening of limb bones [5-7]. We also compared the averaged limb length to the length of the vertebra column as additional measure for possible effects of chondrodysplasia on Niata. In his description, Darwin [8] also stated that frontlimb and hindlimb of the Niata might be disproportional. The relative proportions of the Niata were measured using several postcranial measurements. We compared the proportional length of hindlimbs and frontlimbs as well as the ratio between limbs and body length. For the former, frontlimb length was defined as the sum of lateral lengths of humerus, radius, and metacarpal bone. Hindlimb length was defined as the sum of lateral lengths of femur, tibia, and metatarsal bone. All in all, we measured the legs of 43 adult animals comprising 27 breeds for the comparison of limb length (Supplementary Table 5). Body length was measured in seven mounted skeletons by measuring the distance between the anterior tip of the first cervical vertebra to the posterior tip of the sacrum in midline. This measurement was compared with the averaged limb length of the same skeletons (Supplementary Table 6). Here, frontlimb length was defined as distance between the ventral tip of the third lateral phalange to the dorsalmost point of the superior angulus of the scapula. The hindlimb length is defined as the distance between the ventral tip of the third phalange to the dorsalmost tip of the ilium (Supplementary Figure 4). The results show that the Niata was of comparable weight and height to other cattle breeds (Figure3) as well as there was no disproportional change in frontlimb length to hindlimb length (Supplementary Figure 5). We did also not detect any obvious changes in the length of the appendicular skeleton compared to the axial skeleton (Supplementary Figure 6). Our results show that the Niata exhibits no chondrodysplastic changes to the postcranial skeleton typical for a chondrodysplastic condition [1, 2].



Supplementary Figure 4: Picture of the mounted skeleton MLP 1126. Indicated are the postcranial measurements used to compare height and length of the Niata as well as frontlimb and hindlimb length. I: cervical-sacrum length; II: length frontlimb; length hindlimb; a: anterior length of scapula; b: lateral length of humerus; c: lateral length of radius; d: lateral length of the metacarpal bone; e: length of pelvis; f: lateral length of femur; g: lateral length of tibia; h: lateral length of the metatarsal bone.



Supplementary Figure 5: Results of the comparison between frontlimb and hindlimb length among breeds.



Supplementary Figure 6: Results of the comparison between axial and appendicular skeleton among breeds.

Supplementary Table 4: Body size estimates for the Niata specimen MLP 1126.

source	skeletal part	measurement (cm)	estimated bodyweight (kg)
Scott 1983	humerus length (H2)	32.3	411.63
Anderson et al. 1985	humerus circumference	16.7	
	femur circumference	15.5	545.06
Janis 1990	m1 length	2.2	
	m2 length	2.6	335.48
		Average	430.73
		SD	106.09

Supplementary Table 5: Postcranial measurements to compare frontlimb and hindlimb length between breeds.

Breed	Inventory No.	Sex	Humerus	Radius	Metacarpal	Femur
			length (cm)	length (cm)	length (cm)	length (cm)
Zebu (Indian)	ZNS Haustierkunde B i zb 18	Male	31.5	27	14	37
Angeln	ZNS Haustierkunde B agl 2	Female	30	28.3	20.5	39.7
Zebu (Indian)	ZNS Haustierkunde B i zb 24	Male	35.5	35.2	24	45.5
Angeln	ZNS Haustierkunde B agl 7	Female	30.2	29.5	20.3	40.2
Schwyz (Swiss Brown)	ZNS Haustierkunde B swyz 5	Female	30	27.5	19.8	40
Holland	ZNS Haustierkunde B hld 18	Female	31	28.8	20.1	41.5
Longhorn (British)	ZNS Haustierkunde B lgh 1	Female	30.8	28	19.1	40.9
Longhorn (British)	ZNS Haustierkunde B lgh 3	Female	31.1	28.2	19.5	40.6
Zebu (Indian)	ZNS Haustierkunde B i zb 19	Female	24	24.3	17	31.3
Shorthorn (British)	ZNS Haustierkunde B shh 3	Male	35.8	31.6	20.7	47.7
Shorthorn (British)	ZNS Haustierkunde B shh 121	Female	31.8	29.8	22.7	42
Jersey	ZNS Haustierkunde B jrs 12	Female	27	25.8	18.2	37.2
Jersey	ZNS Haustierkunde B jrs 14	Female	30.1	27	19.8	38.8
Jersey	ZNS Haustierkunde B jrs 13	Female	28.6	26.8	19	37.7
Hereford	ZNS Haustierkunde B hrfd 1	Female	32.4	30.4	22	43.1
Breitenburger	ZNS HaustierkundeB brtb 5	Female	31.9	29.5	21.7	42.7
Jersey	ZNS Haustierkunde B jrs 10	Male	33.8	29.2	19.9	43.3
Vogelsberger	ZNS Haustierkunde B vgb 3	Female	29.6	27.5	19.7	39.7
Vogtländer	ZNS Haustierkunde B vgtl 2	Female	31	29.7	21.5	41.1
Ansbach-Triesdorfer	ZNS Haustierkunde B ans-tr 1	Female	30.2	28.2	21	40.4
Simmental	ZNS Haustierkunde B sim 13	Female	31.5	29.4	21.7	42.3
Silesian Red	ZNS Haustierkunde B sl rtv 2	Female	32.4	29.6	21.5	42.6
Watussi	ZNS Haustierkunde B wa 2	Female	29.8	28.5	19.9	40.1
Hungarian Grey	ZNS Haustierkunde B ug stp 4	?	30.5	29.8	21.2	41.1
Devon	ZNS Haustierkunde B dv 2	Female	26.8	24.8	17.6	35.6
Podolian	ZNS Haustierkunde B pd stp 1	Female	32.2	30.4	20.9	43.3
Prätigauer	ZNS Haustierkunde B prtg 4	Female	33.8	31.2	22.1	45.8
Prätigauer	ZNS Haustierkunde B prtg 3	Female	31.3	29.5	20.8	42.3
Frisian Red	ZNS Haustierkunde B fr r 1	Female	30	28.6	20.9	40
Devon	ZNS Haustierkunde B dv 4	Female	30.4	26.4	18.8	39
Dwarf Zebu	lfH 20159	Female	23.7	22.4	14.7	29.3
Black Pied	lfH 16507	Female	31.7	29.2	20.6	41.6
Black Pied	lfH 24769	Female	30	27.9	19.9	40.3
Heck	lfH 32545	-	32.8	29.8	19.5	41.2
Watussi	lfH 8664	Female	30.8	31.3	21.3	40.2
Watussi	lfH 1574	Male	32.3	31.2	20.9	44.6
Niata	MLP 1126	Male	32.2	29.9	19.5	41.2

Supplementary Table 5 (continued): Postcranial measurements to compare frontlimb and hindlimb length between breeds.

Breed	Inventory No.	Sex	Tibia	Metatar-sal	Frontleg	Hindleg
			length (cm)	length (cm)	length (cm)	length (cm)
Zebu (Indian)	ZNS Haustierkunde B i zb 18	Male	31.8	17.5	72.5	86.3
Angeln	ZNS Haustierkunde B agl 2	Female	32.5	23.5	78.8	95.7
Zebu (Indian)	ZNS Haustierkunde B i zb 24	Male	40	28	94.7	113.5
Angeln	ZNS Haustierkunde B agl 7	Female	33.8	23.2	80	97.2
Schwyz (Swiss Brown)	ZNS Haustierkunde B swyz 5	Female	31.3	22.8	77.3	94.1
Holland	ZNS Haustierkunde B hld 18	Female	32.5	23.5	79.9	97.5
Longhorn (British)	ZNS Haustierkunde B lgh 1	Female	33	22.7	77.9	96.6
Longhorn (British)	ZNS Haustierkunde B lgh 3	Female	32.5	22.5	78.8	95.6
Zebu (Indian)	ZNS Haustierkunde B i zb 19	Female	27.5	20.5	65.3	79.3
Shorthorn (British)	ZNS Haustierkunde B shh 3	Male	34.2	24.9	88.1	106.8
Shorthorn (British)	ZNS Haustierkunde B shh 121	Female	33	26	84.3	101
Jersey	ZNS Haustierkunde B jrs 12	Female	29.4	21	71	87.6
Jersey	ZNS Haustierkunde B jrs 14	Female	32.6	22.9	76.9	94.3
Jersey	ZNS Haustierkunde B jrs 13	Female	31.8	22	74.4	91.5
Hereford	ZNS Haustierkunde B hrfd 1	Female	34.5	24.9	84.8	102.5
Breitenburger	ZNS HaustierkundeB brtb 5	Female	32.5	24.5	83.1	99.7
Jersey	ZNS Haustierkunde B jrs 10	Male	34.6	23.3	82.9	101.2
Vogelsberger	ZNS Haustierkunde B vgb 3	Female	31.9	23	76.8	94.6
Vogtländer	ZNS Haustierkunde B vgtl 2	Female	34.2	25.2	82.2	100.5
Ansbach-Triesdorfer	ZNS Haustierkunde B ans-tr 1	Female	32.5	24	79.4	96.9
Simmental	ZNS Haustierkunde B sim 13	Female	33.7	25	82.6	101
Silesian Red	ZNS Haustierkunde B sl rtv 2	Female	33	24.5	83.5	100.1
Watussi	ZNS Haustierkunde B wa 2	Female	33.9	23.1	78.2	97.1
Hungarian Grey	ZNS Haustierkunde B ug stp 4	?	34.8	25.2	81.5	101.1
Devon	ZNS Haustierkunde B dv 2	Female	28.4	20	69.2	84
Podolian	ZNS Haustierkunde B pd stp 1	Female	33.5	24.3	83.5	101.1
Prätigauer	ZNS Haustierkunde B prtg 4	Female	34.6	24.8	87.1	105.2
Prätigauer	ZNS Haustierkunde B prtg 3	Female	32.3	24	81.6	98.6
Frisian Red	ZNS Haustierkunde B fr r 1	Female	31.3	23.8	79.5	95.1
Devon	ZNS Haustierkunde B dv 4	Female	31	22.1	75.6	92.1
Dwarf Zebu	IfH 20159	Female	24.8	17.5	60.8	71.6
Black Pied	IfH 16507	Female	31.4	23.5	81.5	96.5
Black Pied	IfH 24769	Female	30.5	22.8	77.8	93.6
Heck	IfH 32545	-	33.9	23.2	82.1	98.3
Watussi	IfH 8664	Female	34.4	25	83.4	99.6
Watussi	IfH 1574	Male	34.9	24.4	84.4	103.9
Niata	MLP 1126	Male	33	22.8	81.6	97

Supplementary Table 6: Postcranial measurements to compare axial and appendicular skeleton between breeds.

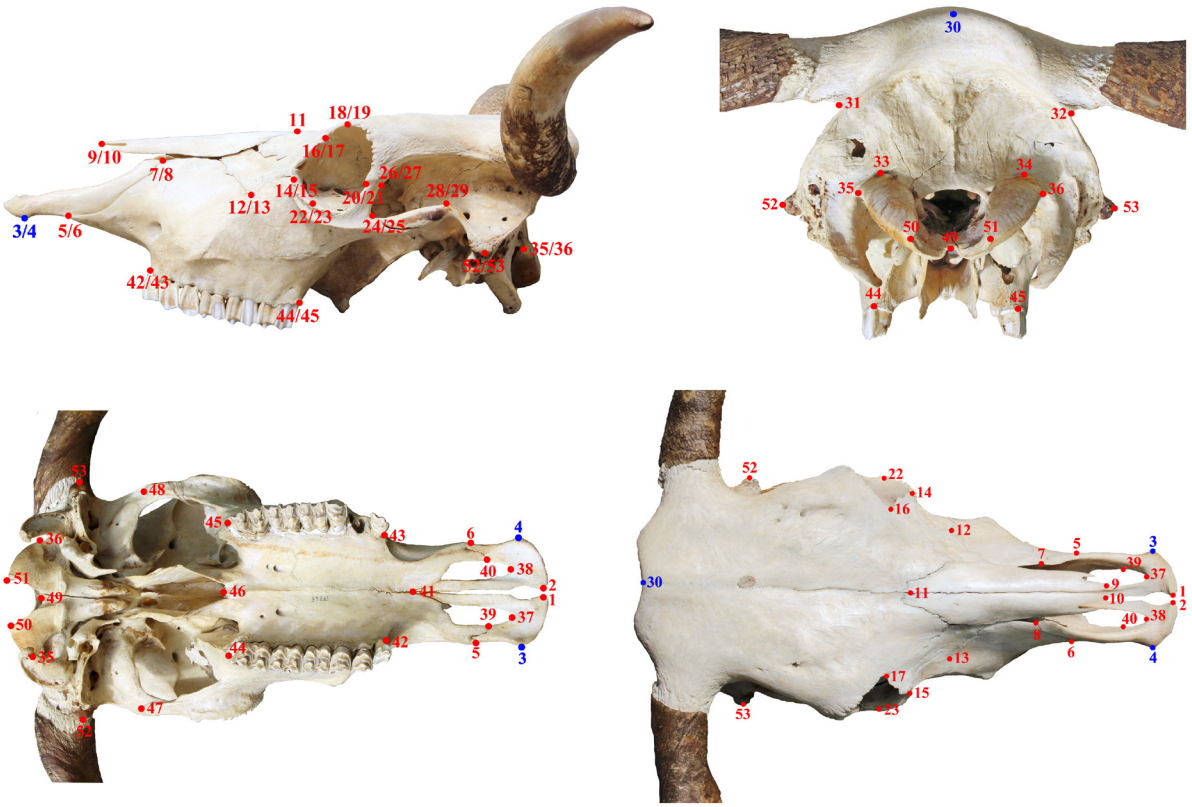
Breed	Ca. No.	Sex	Frontleg (cm)	Hindleg (cm)	Average Leg Length (cm)	Cervical-Sacrum Length (cm)
Kerry	ZNS Haustierkunde B kry 3	Female	89.5	97	93.25	145
Watussi	ZNS Haustierkunde B wa 1	Male	128.5	136.5	132.5	192
Zebu (Indian)	ZNS Haustierkunde B i zb 20	Female	89.7	93.5	91.6	133.5
Indian Dwarf Zebu	ZNS Haustierkunde B zw zb 1	Female	69.5	69	69.25	92
Holland	ZNS Haustierkunde B hld 22	Female	126	136	131	201
Niata	MLP 1126	Male	124.5	127.5	126	197
Red Pied	IfH 7218	Male	124.8	126.6	125.7	212.7

References:

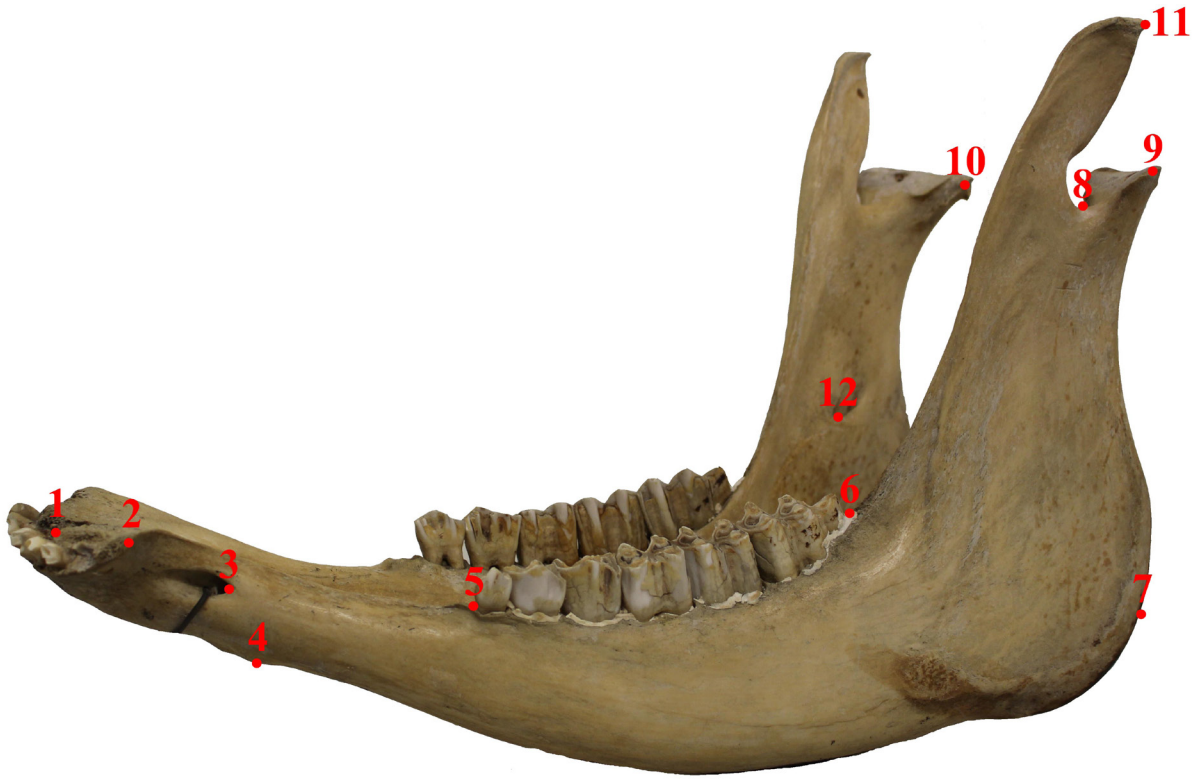
1. Cavanagh JAL, Tammen I, Windsor PA, Bateman JF, Savarirayan R, Nicholas FW, Raadsma HW (2007). Bulldog dwarfism in Dexter cattle is caused by mutations in ACAN. Mamm Genome. 18(11):808-14.
2. Parker HG, VonHoldt BM, Quignon P, Margulies EH, Shao S, Mosher DS, Spady TC, Elkahloun A, Cargill M, Jones PG, Maslen CL, Acland GM, Sutter NB, Kuroki K, Bustamante CD, Wayne RK, Ostrander EA (2009). An expressed fgf4 retrogene is associated with breeddefining chondrodysplasia in domestic dogs. Science. 325(5943):995-8.
3. Felius M (1995). Cattle breeds: an encyclopedia. Doetinchem: Misset.
4. Baldassarre S (1906). La Zootecnia nella repubblica argentina. Atti del Reale Istituto d'Incoraggiamento alle Scienze Naturali di Napoli. 6(58):359-80.
5. Scott KM (1983). Prediction of body weight of fossil Artiodactyla. Zool J Linn Soc. 77(3):199-215.
6. Anderson JF, Hall-Martin A, Russell DA (1985). Long-bone circumference and weight in mammals, birds and dinosaurs. J Zool. 207(1):53-61.
7. Janis CM (1990). Correlation of cranial and dental variables with body size in ungulates and macropodoids. In: Damuth JD, MacFadden BJ, editors. Body Size in Mammalian Paleobiology: Estimation and Biological Implications. Cambridge: Cambridge University Press; p. 255-99.
8. Darwin C (1845). Journal of researches into the geology and natural history of the various countries visited by H.M.S. Beagle round the world, under the Command of Capt. Fitz Roy, R.N. 2nd edition. London: John Murray.

Geometric morphometrics

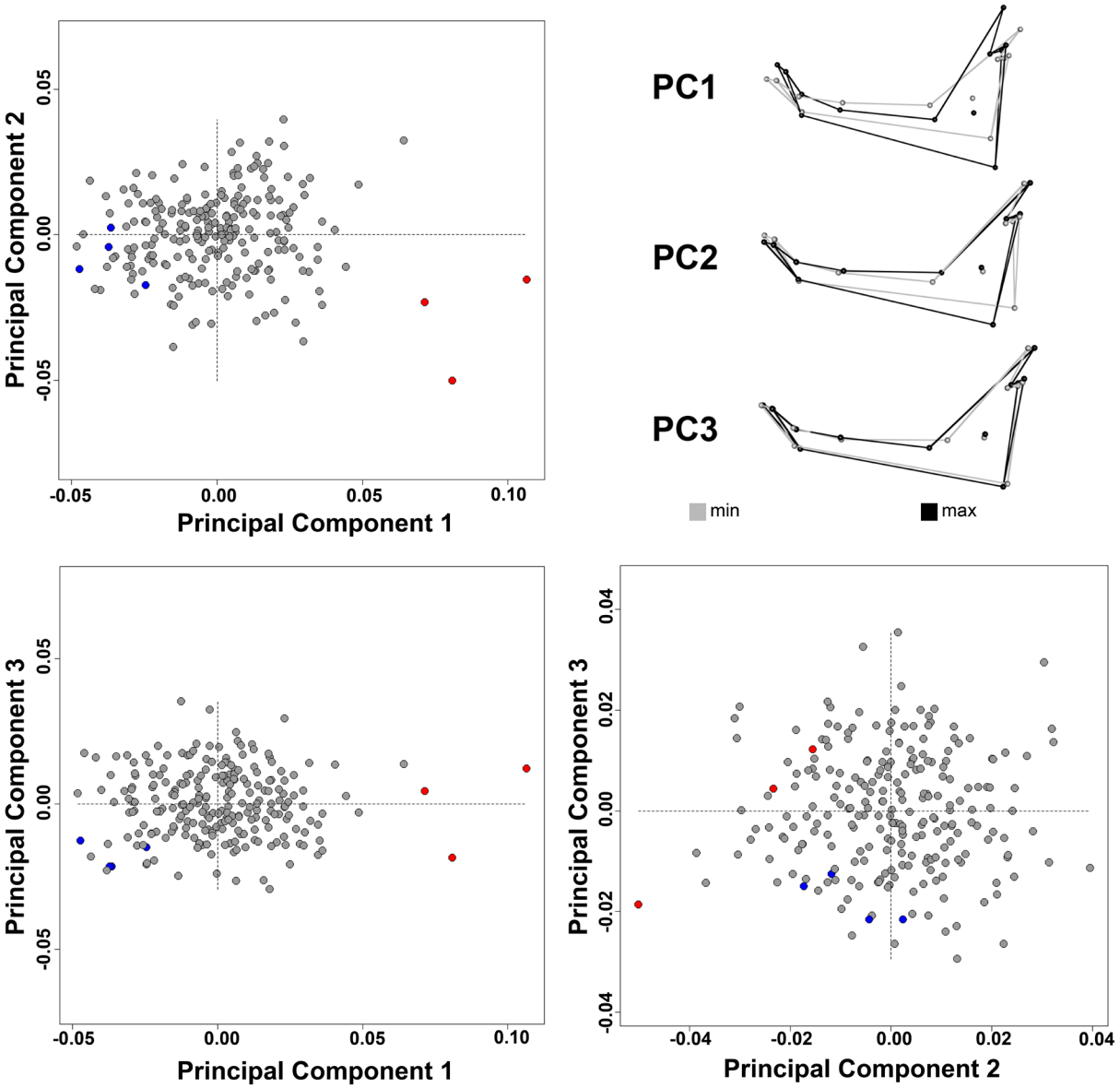
On the skull we digitized 53 landmarks (Supplementary Figure 7, Supplementary Table 7). Custom frame was used in MUS 6.0.1 to acquire landmarks on the dorsal and ventral part of the skull. Three reference landmarks (3, 4, and 30) were taken to set the frame and, after turning the skull, the same three reference landmarks were taken (Supplementary Figure 7). With this, the complete skull was landmarked. On the lower jaw we digitized 12 landmarks using the default setting for the frame (Supplementary Figure 8, Supplementary Table 8). The shape of the lower jaw was analyzed using the same procedure as described for the skulls in the main text. The first three PC-axes of the PCA on lower jaws reflects 52 percent of the overall shape variation (Supplementary Figure 10). PC-axis 1 reflects 30 percent, PC-axis 2 13 percent, and PC-axis 3 9 percent of the overall shape variation. The shape changes of the lower jaw in PC1-axis reflect the Niata condition. On the positive side of the axis the lower jaw is curved upwards. The second PC-axis is mostly defined by landmark 7 reflecting the difference in curvature of the angulus in cattle. The axis of PC3 shows the different extensions of the dental row. We used Procrustes distances to assess the difference among shapes by breed (Supplementary Table 9, Supplementary Table 10). The distances in skulls are extensively discussed in the main text. In the lower jaw the Niata are most different from *Bos primigenius* (PD: 0.18), Heck (PD: 0.15), and Walchshofer (PD: 0.15). These distances are shorter than observed in the skulls. However, the closest breeds to the Niata in lower jaw shape are further removed than in skulls. These close breeds are Vogtlaender (PD: 0.09), Normand (PD: 0.09), and Tuxer (PD: 0.10).



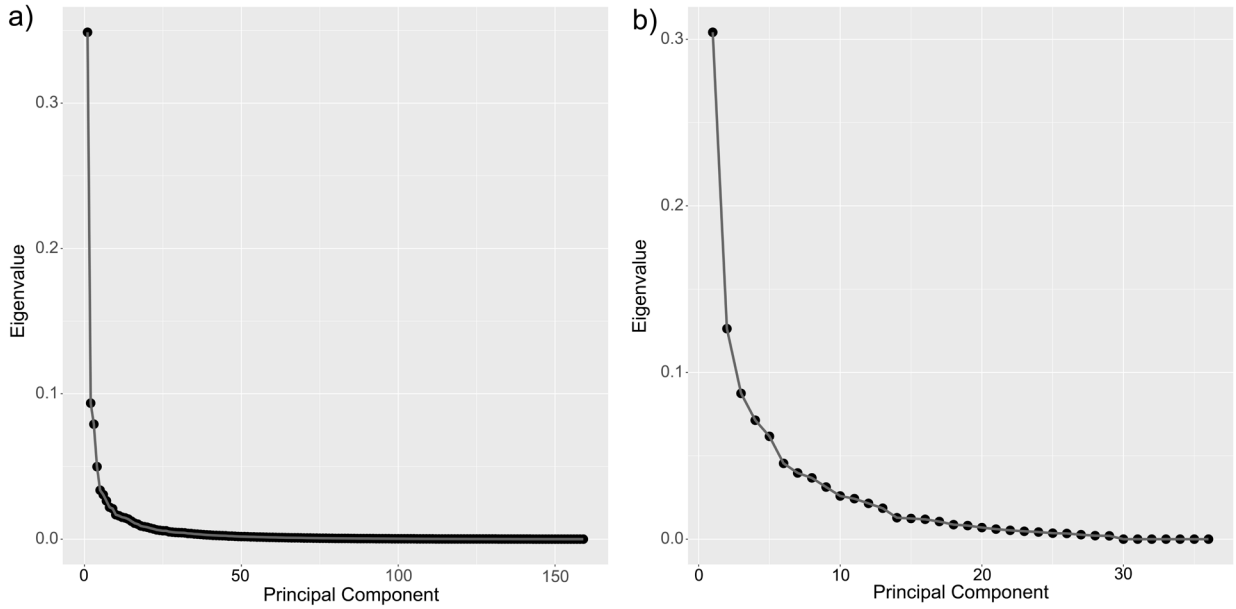
Supplementary Figure 7: Landmarks on the skull used in this study. Indicated in blue are the landmarks used for custom frame to rotate the skull.



Supplementary Figure 8: Landmarks on the lower jaw used in this study.



Supplementary Figure 9: Principal Component Analysis of the lower jaw shapes of different cattle breeds. Top left, bottom left and bottom right are the comparisons between PC1, PC2, and PC3. Top right are the associated shape changes.



Supplementary Figure 10: Eigenvalues of the PC-axes from PCA on the skulls (a) and lower jaws (b) of different cattle breeds.

Supplementary Table 7: Definition of the landmarks used on the skull in this study.

LM	Definition
1	Medialmost point of the alveolar process (premaxilla) sin
2	Medialmost point of the alveolar process (premaxilla) dext
3	Lateralmost point of the anterior part of the premaxilla sin
4	Lateralmost point of the anterior part of the premaxilla dext
5	Inferior-lateral sutureboarder between premaxilla and maxilla sin
6	Inferior-lateral sutureboarder between premaxilla and maxilla dxt
7	Superior-posteriormost point of the premaxillary bone (nasal process) sin
8	Superior-posteriormost point of the premaxillary bone (nasal process) dxt
9	Anteriormost point of the medial processus of the nasal bone sin
10	Anteriormost point of the medial processus of the nasal bone dxt
11	Medial boarder between nasal bone and frontal bone
12	Boarder between lacrimal, maxillar and zygomatic bone sin
13	Boarder between lacrimal, maxillar and zygomatic bone dxt
14	Inferior suture between lacrimal bone and orbit sin
15	Inferior suture between lacrimal bone and orbit dxt
16	Superior suture between lacrimal bone and orbit sin
17	Superior suture between lacrimal bone and orbit dxt
18	Superiormost point of the orbit sin
19	Superiormost point of the orbit dxt
20	Boarder between frontal and temporal bone in the orbit sin
21	Boarder between frontal and temporal bone in the orbit dxt
22	Inferiormost point of the orbit sin
23	Inferiormost point of the orbit dxt
24	Anteriormost point of the zygomatic bone behind the orbit sin
25	Anteriormost point of the zygomatic bone behind the orbit dxt
26	Boarder between frontal and temporal bone behind the orbit sin
27	Boarder between frontal and temporal bone behind the orbit dxt
28	Superiormost point of the zygomatic arch sin
29	Superiormost point of the zygomatic arch dxt
30	Posteriormost point of the frontal bone in the midline
31	Medial-posteriormost point of the fossa temporalis sin
32	Medial-posteriormost point of the fossa temporalis dxt
33	Superiormost point of the occipital articulation surface sin
34	Superiormost point of the occipital articulation surface dxt
35	Lateralmost point of the occipital articulation surface sin
36	Lateralmost point of the occipital articulation surface dxt
Skull turned around	
37	Anteriormost point of the palatine fissure sin
38	Anteriormost point of the palatine fissure dext
39	Inferior-medial sutureborder between premaxilla and maxilla sin
40	Inferior-medial sutureborder between premaxilla and maxilla dxt
41	Inferior-medial sutureborder between premaxilla (palatine process) and maxilla
42	Anterior boarder of premolar 2 sin
43	Anterior boarder of premolar 2 dext

44	Posterior boarder of molar 3 sin
45	Posterior boarder of molar 3 dext
46	Posteriormost point of the horizontal part of the palatal bone (in the midline)
47	Posteriormost suturepoint between zygomatic and temporal bone from ventral sin
48	Posteriormost suturepoint between zygomatic and temporal bone from ventral dxt
49	Inferior-medial boarder of the foramen magnum
50	Medialmost point of the flexure between dorsal and ventral part of the occipital articulation surface sin
51	Medialmost point of the flexure between dorsal and ventral part of the occipital articulation surface dxt
52	Tip of the notch above the opening of the acoustic canal sin
53	Tip of the notch above the opening of the acoustic canal dxt

Supplementary Table 8: Definition of the landmarks used on the lower jaw in this study.

LM	**Definition**
1	Medial boarder between bone and root of I1 sin.
2	Lateralmost point of the incisor-shovel sin.
3	Posterior boarder of the mental foramen sin.
4	Ventralmost point of the posterior beginning of the symphysis sin.
5	Anterior boarder mandibel and premolar 2 sin
6	Posterior boarder mandibel and molar 3 sin
7	Middlepoint of curvature of the angulus sin.
8	Ventralmost midpoint of the mandibular notch sin.
9	Lateralmost point of the condylar process sin.
10	Medialmost point of the condylar process sin.
11	Tip of thr coronoid process sin.
12	Ventral boarder of the mandibular foramen sin.

Supplementary Table 9: Procrustes distances among skulls from cattle breeds represented in morphospace.

	Ayrshire	Blondvieh: Carinthian	Blondvieh: Lavanttaler	Blondvieh: Mariahofer	Blondvieh: Murbodner	Blondvieh: Waldviertler
Ayrshire		0.041	0.046	0.048	0.042	0.041
Blondvieh: Carinthian	0.041		0.023	0.044	0.022	0.024
Blondvieh: Lavanttaler	0.046	0.023		0.040	0.030	0.029
Blondvieh: Mariahofer	0.048	0.044	0.040		0.045	0.047
Blondvieh: Murbodner	0.042	0.022	0.030	0.045		0.032
Blondvieh: Waldviertler	0.041	0.024	0.029	0.047	0.032	
Bos primigenius (Aurochs)	0.071	0.061	0.059	0.074	0.061	0.057
Brazilian	0.057	0.049	0.050	0.048	0.044	0.051
Montafon	0.046	0.020	0.025	0.044	0.024	0.024
Buša	0.046	0.039	0.037	0.050	0.042	0.028
Chianina	0.057	0.043	0.043	0.060	0.046	0.038
Chillingham	0.063	0.068	0.065	0.064	0.070	0.060
Devon	0.033	0.034	0.038	0.039	0.033	0.036
Egerlaender	0.061	0.038	0.036	0.056	0.041	0.044
Hérens	0.042	0.056	0.055	0.048	0.053	0.053
Fjällko	0.039	0.029	0.034	0.052	0.038	0.025
Bern Red Pied	0.045	0.019	0.024	0.044	0.024	0.028
Freiburg Red Pied	0.058	0.043	0.048	0.054	0.043	0.047
Simmental	0.042	0.040	0.043	0.040	0.038	0.042
South Moravian Red Pied	0.045	0.026	0.029	0.042	0.030	0.034
Rubia Gallega	0.075	0.054	0.060	0.079	0.053	0.051
Allgaeuer Grey	0.055	0.044	0.046	0.040	0.046	0.046
Krainer Grey	0.046	0.044	0.047	0.053	0.040	0.041
Oberinntaler Grey	0.033	0.030	0.032	0.041	0.029	0.032
Haná-Berne	0.055	0.031	0.036	0.056	0.034	0.031
Iceland	0.033	0.049	0.054	0.055	0.049	0.045
Jersey	0.049	0.067	0.067	0.051	0.065	0.067
Jersey (polled)	0.047	0.063	0.065	0.048	0.059	0.064
Jutland	0.053	0.036	0.039	0.062	0.044	0.031
Kampeten: Styrian Bergscheck	0.035	0.031	0.029	0.035	0.032	0.029
Kampeten: Welser Schecken	0.062	0.046	0.047	0.059	0.048	0.044
Kerry	0.035	0.033	0.038	0.052	0.038	0.027
Cretan	0.064	0.059	0.055	0.057	0.060	0.049
Kuhlaender	0.041	0.020	0.026	0.042	0.021	0.022
Landschlag von Warnsdorf	0.053	0.047	0.052	0.049	0.045	0.050
Landschlag von Winkelsdorf	0.069	0.041	0.044	0.066	0.049	0.042
Landschlag X Simmental	0.057	0.034	0.037	0.056	0.035	0.040
Limousin	0.040	0.040	0.045	0.040	0.035	0.048
Moravian Landschlag	0.043	0.036	0.043	0.042	0.034	0.038
Normande	0.040	0.046	0.044	0.038	0.046	0.053
North Wales	0.040	0.027	0.033	0.043	0.028	0.025
White Park	0.055	0.059	0.059	0.058	0.062	0.050
Pinzgauer	0.035	0.029	0.036	0.037	0.024	0.034
Pinzgauer X Scottish Highland	0.059	0.054	0.051	0.053	0.048	0.061

Pinzgauer X Simmentaler	0.051	0.062	0.063	0.053	0.053	0.061
Pinzgauer: Moelltaler	0.051	0.027	0.032	0.045	0.027	0.030
Pinzgauer: Pustertaler	0.072	0.075	0.071	0.059	0.072	0.075
Pirenaica	0.033	0.035	0.039	0.036	0.038	0.036
Red Poll	0.063	0.070	0.070	0.053	0.069	0.070
Maas-Rhein-Ijsselschlag	0.033	0.027	0.031	0.037	0.030	0.027
Danish Red	0.049	0.028	0.030	0.051	0.038	0.030
Angeln	0.043	0.041	0.040	0.045	0.038	0.038
Bohemian Red	0.041	0.019	0.024	0.043	0.023	0.020
Polish Red	0.053	0.033	0.036	0.055	0.039	0.027
Sanga	0.083	0.061	0.060	0.080	0.068	0.059
Sardinian	0.057	0.042	0.041	0.060	0.047	0.046
Scheinfelder	0.059	0.043	0.043	0.056	0.043	0.042
Schoenhengster	0.047	0.022	0.025	0.047	0.025	0.023
Holland Black Pied	0.046	0.043	0.045	0.041	0.045	0.043
Andalusian Black	0.053	0.035	0.034	0.053	0.039	0.033
Sweden (Jaemtland or Vatterbotten)	0.058	0.059	0.060	0.075	0.065	0.060
Scottish Highland	0.050	0.057	0.060	0.050	0.050	0.056
Sicilian	0.062	0.058	0.058	0.062	0.052	0.064
Småland	0.053	0.044	0.048	0.066	0.050	0.036
South Devon	0.046	0.026	0.035	0.052	0.031	0.029
Spanish Fighting Cattle	0.054	0.059	0.057	0.051	0.058	0.060
Buchara Grey	0.127	0.103	0.104	0.122	0.108	0.098
Hungarian Grey	0.044	0.036	0.042	0.042	0.031	0.043
Hungarian Grey X Bern Red Pied	0.067	0.066	0.072	0.066	0.063	0.070
Sudeten	0.044	0.031	0.037	0.047	0.036	0.031
Sudeten X Simmental	0.042	0.049	0.047	0.046	0.052	0.052
Sudeten X Tesstal?	0.051	0.040	0.046	0.048	0.040	0.047
Tarentaise	0.043	0.047	0.041	0.041	0.048	0.044
Telemark	0.036	0.034	0.037	0.050	0.035	0.024
Tudanca	0.054	0.037	0.040	0.052	0.040	0.034
Tuxer	0.081	0.090	0.088	0.067	0.085	0.090
Heck	0.037	0.040	0.044	0.048	0.038	0.034
Niata	0.200	0.218	0.217	0.192	0.210	0.221
Veredelter Landschlag	0.054	0.042	0.045	0.059	0.041	0.044
Vogtlaender	0.037	0.042	0.045	0.040	0.038	0.048
Waldviertler X Scheinfelder	0.044	0.036	0.036	0.039	0.041	0.039
Watussi	0.055	0.039	0.044	0.061	0.041	0.045
Zebu	0.068	0.051	0.051	0.072	0.058	0.045
Zebu (Africa)	0.067	0.060	0.062	0.078	0.056	0.057
Zebu (Asian)	0.053	0.055	0.056	0.058	0.052	0.055
Zebu (Indian)	0.070	0.050	0.050	0.067	0.055	0.046
Zillertaler	0.051	0.059	0.058	0.043	0.055	0.058
	Bos primigenius (Aurochs)	Brazilian	Montafon	Buša	Chianina	Chillingham

Ayrshire	0.071	0.057	0.046	0.046	0.057	0.063
Blondvieh: Carinthian	0.061	0.049	0.020	0.039	0.043	0.068
Blondvieh: Lavanttaler	0.059	0.050	0.025	0.037	0.043	0.065
Blondvieh: Mariahofer	0.074	0.048	0.044	0.050	0.060	0.064
Blondvieh: Murbodner	0.061	0.044	0.024	0.042	0.046	0.070
Blondvieh: Waldviertler	0.057	0.051	0.024	0.028	0.038	0.060
Bos primigenius (Aurochs)		0.058	0.055	0.063	0.057	0.079
Brazilian	0.058		0.043	0.056	0.054	0.070
Montafon	0.055	0.043		0.034	0.039	0.064
Buša	0.063	0.056	0.034		0.047	0.056
Chianina	0.057	0.054	0.039	0.047		0.075
Chillingham	0.079	0.070	0.064	0.056	0.075	
Devon	0.072	0.045	0.036	0.040	0.048	0.064
Egerlaender	0.070	0.061	0.039	0.053	0.055	0.086
Hérens	0.080	0.058	0.055	0.050	0.073	0.054
Fjällko	0.065	0.060	0.034	0.029	0.047	0.065
Bern Red Pied	0.059	0.046	0.020	0.039	0.043	0.069
Freiburg Red Pied	0.065	0.050	0.043	0.063	0.049	0.081
Simmental	0.066	0.036	0.038	0.049	0.054	0.063
South Moravian Red Pied	0.057	0.042	0.028	0.046	0.046	0.067
Rubia Gallega	0.064	0.063	0.048	0.056	0.051	0.086
Allgaeuer Grey	0.064	0.046	0.044	0.055	0.063	0.065
Krainer Grey	0.065	0.050	0.044	0.053	0.048	0.073
Oberinntaler Grey	0.060	0.049	0.030	0.040	0.051	0.059
Haná-Berne	0.051	0.052	0.031	0.047	0.044	0.076
Iceland	0.075	0.061	0.052	0.045	0.065	0.058
Jersey	0.100	0.072	0.071	0.066	0.080	0.077
Jersey (polled)	0.094	0.067	0.064	0.062	0.076	0.074
Jutland	0.056	0.061	0.036	0.037	0.042	0.067
Kampeten: Styrian Bergscheck	0.056	0.045	0.029	0.034	0.050	0.056
Kampeten: Welser Schecken	0.044	0.055	0.042	0.055	0.049	0.074
Kerry	0.061	0.053	0.032	0.026	0.046	0.055
Cretan	0.077	0.057	0.054	0.041	0.049	0.068
Kuhlaender	0.059	0.046	0.023	0.036	0.040	0.066
Landschlag von Warnsdorf	0.086	0.057	0.052	0.051	0.066	0.077
Landschlag von Winkelsdorf	0.063	0.064	0.043	0.052	0.050	0.083
Landschlag X Simmental	0.068	0.057	0.033	0.045	0.052	0.074
Limousin	0.079	0.045	0.044	0.054	0.059	0.075
Moravian Landschlag	0.070	0.049	0.039	0.045	0.055	0.067
Normande	0.084	0.057	0.050	0.060	0.061	0.077
North Wales	0.062	0.041	0.027	0.035	0.039	0.058
White Park	0.084	0.070	0.058	0.041	0.068	0.060
Pinzgauer	0.067	0.042	0.031	0.044	0.046	0.065
Pinzgauer X Scottish Highland	0.074	0.065	0.053	0.065	0.075	0.078
Pinzgauer X Simmentaler	0.089	0.061	0.063	0.067	0.073	0.075
Pinzgauer: Moelltaler	0.060	0.040	0.024	0.042	0.035	0.069
Pinzgauer: Pustertaler	0.084	0.068	0.071	0.078	0.082	0.078

Pirenaica	0.071	0.043	0.038	0.042	0.049	0.061
Red Poll	0.083	0.058	0.069	0.070	0.082	0.066
Maas-Rhein-Ijsselschlag	0.066	0.048	0.029	0.031	0.043	0.063
Danish Red	0.068	0.062	0.033	0.039	0.049	0.072
Angeln	0.059	0.045	0.037	0.036	0.051	0.055
Bohemian Red	0.059	0.049	0.022	0.032	0.042	0.067
Polish Red	0.065	0.058	0.032	0.028	0.043	0.065
Sanga	0.074	0.078	0.058	0.058	0.062	0.086
Sardinian	0.070	0.061	0.043	0.055	0.051	0.081
Scheinfelder	0.061	0.050	0.040	0.043	0.051	0.073
Schoenhengster	0.057	0.049	0.020	0.035	0.042	0.067
Holland Black Pied	0.061	0.044	0.043	0.049	0.057	0.061
Andalusian Black	0.044	0.044	0.028	0.037	0.044	0.064
Sweden (Jaemtland or Vatterbotten)	0.086	0.091	0.064	0.059	0.080	0.086
Scottish Highland	0.075	0.046	0.054	0.060	0.068	0.063
Sicilian	0.069	0.058	0.059	0.073	0.072	0.091
Småland	0.068	0.067	0.044	0.036	0.054	0.063
South Devon	0.065	0.050	0.028	0.038	0.036	0.071
Spanish Fighting Cattle	0.066	0.050	0.055	0.059	0.075	0.056
Buchara Grey	0.106	0.112	0.098	0.099	0.092	0.117
Hungarian Grey	0.067	0.033	0.037	0.051	0.051	0.069
Hungarian Grey X Bern Red Pied	0.080	0.048	0.067	0.077	0.073	0.089
Sudeten	0.065	0.052	0.037	0.044	0.048	0.069
Sudeten X Simmental	0.088	0.069	0.056	0.055	0.071	0.068
Sudeten X Tesstal?	0.071	0.048	0.044	0.055	0.055	0.078
Tarentaise	0.068	0.056	0.046	0.045	0.063	0.054
Telemark	0.059	0.054	0.034	0.031	0.040	0.060
Tudanca	0.055	0.046	0.033	0.042	0.036	0.068
Tuxer	0.102	0.076	0.088	0.092	0.099	0.084
Heck	0.065	0.044	0.039	0.039	0.047	0.055
Niata	0.236	0.199	0.218	0.221	0.226	0.210
Veredelter Landschlag	0.070	0.059	0.044	0.049	0.059	0.072
Vogtlaender	0.079	0.051	0.047	0.056	0.064	0.073
Waldviertler X Scheinfelder	0.075	0.054	0.041	0.044	0.061	0.063
Watussi	0.067	0.062	0.042	0.053	0.059	0.083
Zebu	0.074	0.073	0.048	0.041	0.053	0.076
Zebu (Africa)	0.075	0.070	0.057	0.054	0.069	0.085
Zebu (Asian)	0.079	0.060	0.057	0.060	0.055	0.081
Zebu (Indian)	0.071	0.065	0.045	0.050	0.045	0.080
Zillertaler	0.080	0.053	0.058	0.064	0.068	0.070

	Devon	Egerlaender	Hérens	Fjällko	Bern Red Pied	Freiburg Red Pied
Ayrshire	0.033	0.061	0.042	0.039	0.045	0.058
Blondvieh: Carinthian	0.034	0.038	0.056	0.029	0.019	0.043
Blondvieh: Lavanttaler	0.038	0.036	0.055	0.034	0.024	0.048
Blondvieh: Mariahofer	0.039	0.056	0.048	0.052	0.044	0.054

Blondvieh: Murbodner	0.033	0.041	0.053	0.038	0.024	0.043
Blondvieh: Waldviertler	0.036	0.044	0.053	0.025	0.028	0.047
Bos primigenius (Aurochs)	0.072	0.070	0.080	0.065	0.059	0.065
Brazilian	0.045	0.061	0.058	0.060	0.046	0.050
Montafon	0.036	0.039	0.055	0.034	0.020	0.043
Buša	0.040	0.053	0.050	0.029	0.039	0.063
Chianina	0.048	0.055	0.073	0.047	0.043	0.049
Chillingham	0.064	0.086	0.054	0.065	0.069	0.081
Devon		0.052	0.044	0.036	0.035	0.050
Egerlaender	0.052		0.071	0.048	0.035	0.053
Hérens	0.044	0.071		0.054	0.055	0.067
Fjällko	0.036	0.048	0.054		0.034	0.057
Bern Red Pied	0.035	0.035	0.055	0.034		0.040
Freiburg Red Pied	0.050	0.053	0.067	0.057	0.040	
Simmental	0.035	0.056	0.040	0.050	0.037	0.044
South Moravian Red Pied	0.041	0.046	0.052	0.042	0.029	0.045
Rubia Gallega	0.064	0.062	0.087	0.060	0.054	0.063
Allgaeuer Grey	0.049	0.057	0.054	0.055	0.045	0.050
Krainer Grey	0.046	0.059	0.058	0.051	0.047	0.046
Oberinntaler Grey	0.035	0.048	0.041	0.036	0.029	0.046
Haná-Berne	0.049	0.042	0.065	0.040	0.032	0.044
Iceland	0.041	0.071	0.042	0.041	0.052	0.067
Jersey	0.049	0.080	0.050	0.063	0.070	0.076
Jersey (polled)	0.048	0.079	0.051	0.064	0.065	0.074
Jutland	0.051	0.054	0.068	0.031	0.040	0.058
Kampeten: Styrian Bergscheck	0.034	0.048	0.040	0.037	0.029	0.049
Kampeten: Welser Schecken	0.061	0.058	0.072	0.056	0.044	0.052
Kerry	0.034	0.055	0.048	0.024	0.036	0.056
Cretan	0.049	0.069	0.067	0.054	0.060	0.070
Kuhlaender	0.032	0.040	0.052	0.032	0.024	0.044
Landschlag von Warnsdorf	0.039	0.057	0.051	0.048	0.050	0.060
Landschlag von Winkelsdorf	0.061	0.049	0.080	0.047	0.043	0.061
Landschlag X Simmental	0.047	0.040	0.067	0.044	0.034	0.059
Limousin	0.029	0.056	0.050	0.049	0.043	0.050
Moravian Landschlag	0.036	0.056	0.049	0.044	0.041	0.051
Normande	0.036	0.058	0.053	0.053	0.048	0.059
North Wales	0.027	0.049	0.049	0.035	0.030	0.044
White Park	0.047	0.071	0.051	0.045	0.061	0.076
Pinzgauer	0.025	0.050	0.044	0.041	0.031	0.039
Pinzgauer X Scottish Highland	0.060	0.056	0.062	0.066	0.050	0.066
Pinzgauer X Simmentaler	0.047	0.074	0.045	0.068	0.061	0.059
Pinzgauer: Moelltaler	0.035	0.042	0.060	0.041	0.025	0.039
Pinzgauer: Pustertaler	0.073	0.083	0.066	0.084	0.072	0.079
Pirenaica	0.030	0.057	0.045	0.042	0.040	0.050
Red Poll	0.062	0.086	0.055	0.075	0.069	0.077
Maas-Rhein-Ijsselschlag	0.024	0.047	0.046	0.026	0.031	0.049
Danish Red	0.043	0.039	0.065	0.029	0.032	0.056

Angeln	0.037	0.057	0.040	0.042	0.040	0.054
Bohemian Red	0.034	0.037	0.051	0.027	0.022	0.044
Polish Red	0.043	0.049	0.063	0.030	0.038	0.061
Sanga	0.072	0.062	0.093	0.061	0.062	0.081
Sardinian	0.051	0.049	0.076	0.051	0.044	0.062
Scheinfelder	0.046	0.051	0.064	0.047	0.040	0.056
Schoenhengster	0.039	0.038	0.053	0.032	0.021	0.044
Holland Black Pied	0.044	0.061	0.046	0.049	0.044	0.052
Andalusian Black	0.045	0.046	0.061	0.041	0.032	0.050
Sweden (Jaemtland or Vatterbotten)	0.066	0.065	0.072	0.045	0.062	0.082
Scottish Highland	0.048	0.075	0.042	0.064	0.057	0.060
Sicilian	0.061	0.064	0.067	0.067	0.058	0.064
Småland	0.052	0.061	0.064	0.033	0.048	0.067
South Devon	0.031	0.045	0.062	0.030	0.031	0.048
Spanish Fighting Cattle	0.056	0.075	0.045	0.065	0.058	0.068
Buchara Grey	0.113	0.106	0.135	0.105	0.103	0.112
Hungarian Grey	0.031	0.054	0.049	0.048	0.036	0.042
Hungarian Grey X Bern Red Pied	0.059	0.078	0.068	0.076	0.067	0.062
Sudeten	0.040	0.047	0.054	0.035	0.037	0.046
Sudeten X Simmental	0.045	0.064	0.043	0.048	0.053	0.067
Sudeten X Tesstal?	0.040	0.056	0.058	0.048	0.043	0.050
Tarentaise	0.047	0.061	0.041	0.051	0.046	0.061
Telemark	0.034	0.054	0.050	0.027	0.036	0.051
Tudanca	0.046	0.052	0.064	0.040	0.037	0.049
Tuxer	0.079	0.102	0.064	0.097	0.088	0.089
Heck	0.031	0.059	0.044	0.040	0.042	0.048
Niata	0.200	0.226	0.183	0.224	0.217	0.210
Veredelter Landschlag	0.048	0.057	0.060	0.047	0.046	0.060
Vogtlaender	0.035	0.058	0.040	0.051	0.044	0.050
Waldviertler X Scheinfelder	0.035	0.053	0.047	0.041	0.037	0.055
Watussi	0.048	0.047	0.069	0.046	0.039	0.057
Zebu	0.057	0.058	0.078	0.045	0.052	0.073
Zebu (Africa)	0.060	0.069	0.072	0.057	0.058	0.075
Zebu (Asian)	0.045	0.066	0.068	0.058	0.056	0.063
Zebu (Indian)	0.056	0.053	0.079	0.054	0.049	0.063
Zillertaler	0.051	0.073	0.043	0.067	0.059	0.061
	Simmental	South Moravian Red Pied	Rubia Gallega	Allgaeuer Grey	Krainer Grey	Oberinntaler Grey
Ayrshire	0.042	0.045	0.075	0.055	0.046	0.033
Blondvieh: Carinthian	0.040	0.026	0.054	0.044	0.044	0.030
Blondvieh: Lavanttaler	0.043	0.029	0.060	0.046	0.047	0.032
Blondvieh: Mariahofer	0.040	0.042	0.079	0.040	0.053	0.041
Blondvieh: Murbodner	0.038	0.030	0.053	0.046	0.040	0.029
Blondvieh: Waldviertler	0.042	0.034	0.051	0.046	0.041	0.032
Bos primigenius (Aurochs)	0.066	0.057	0.064	0.064	0.065	0.060

Brazilian	0.036	0.042	0.063	0.046	0.050	0.049
Montafon	0.038	0.028	0.048	0.044	0.044	0.030
Buša	0.049	0.046	0.056	0.055	0.053	0.040
Chianina	0.054	0.046	0.051	0.063	0.048	0.051
Chillingham	0.063	0.067	0.086	0.065	0.073	0.059
Devon	0.035	0.041	0.064	0.049	0.046	0.035
Egerlaender	0.056	0.046	0.062	0.057	0.059	0.048
Hérens	0.040	0.052	0.087	0.054	0.058	0.041
Fjällko	0.050	0.042	0.060	0.055	0.051	0.036
Bern Red Pied	0.037	0.029	0.054	0.045	0.047	0.029
Freiburg Red Pied	0.044	0.045	0.063	0.050	0.046	0.046
Simmental		0.032	0.070	0.040	0.045	0.033
South Moravian Red Pied	0.032		0.062	0.041	0.044	0.031
Rubia Gallega	0.070	0.062		0.075	0.063	0.065
Allgaeuer Grey	0.040	0.041	0.075		0.055	0.044
Krainer Grey	0.045	0.044	0.063	0.055		0.042
Oberinntaler Grey	0.033	0.031	0.065	0.044	0.042	
Haná-Berne	0.047	0.036	0.050	0.052	0.047	0.038
Iceland	0.044	0.051	0.078	0.059	0.053	0.039
Jersey	0.057	0.068	0.100	0.067	0.065	0.060
Jersey (polled)	0.053	0.062	0.092	0.065	0.060	0.053
Jutland	0.059	0.047	0.053	0.061	0.055	0.046
Kampeten: Styrian Bergscheck	0.032	0.029	0.066	0.038	0.043	0.019
Kampeten: Welser Schecken	0.052	0.041	0.058	0.055	0.051	0.046
Kerry	0.043	0.042	0.055	0.055	0.047	0.032
Cretan	0.060	0.061	0.065	0.065	0.063	0.063
Kuhlaender	0.037	0.027	0.054	0.044	0.041	0.029
Landschlag von Warnsdorf	0.047	0.051	0.076	0.054	0.057	0.050
Landschlag von Winkelsdorf	0.064	0.048	0.056	0.061	0.064	0.057
Landschlag X Simmental	0.054	0.043	0.053	0.060	0.058	0.044
Limousin	0.034	0.042	0.073	0.050	0.049	0.041
Moravian Landschlag	0.035	0.036	0.067	0.043	0.046	0.035
Normande	0.046	0.047	0.083	0.058	0.054	0.046
North Wales	0.035	0.035	0.050	0.047	0.040	0.034
White Park	0.057	0.064	0.078	0.066	0.069	0.057
Pinzgauer	0.027	0.031	0.064	0.041	0.035	0.026
Pinzgauer X Scottish Highland	0.061	0.052	0.086	0.057	0.064	0.049
Pinzgauer X Simmentaler	0.047	0.061	0.089	0.059	0.057	0.052
Pinzgauer: Moelltaler	0.037	0.031	0.049	0.045	0.043	0.037
Pinzgauer: Pustertaler	0.062	0.066	0.102	0.063	0.072	0.062
Pirenaica	0.033	0.035	0.067	0.047	0.040	0.036
Red Poll	0.053	0.059	0.098	0.055	0.069	0.060
Maas-Rhein-Ijsselschlag	0.037	0.036	0.060	0.046	0.043	0.032
Danish Red	0.057	0.044	0.057	0.056	0.055	0.043
Angeln	0.035	0.039	0.065	0.045	0.048	0.035
Bohemian Red	0.037	0.027	0.054	0.044	0.042	0.026
Polish Red	0.053	0.042	0.051	0.058	0.056	0.044

Sanga	0.084	0.072	0.058	0.082	0.081	0.073
Sardinian	0.062	0.052	0.059	0.066	0.058	0.052
Scheinfelder	0.048	0.048	0.050	0.058	0.056	0.047
Schoenhengster	0.037	0.028	0.052	0.046	0.042	0.029
Holland Black Pied	0.034	0.034	0.074	0.041	0.047	0.038
Andalusian Black	0.043	0.038	0.047	0.052	0.051	0.039
Sweden (Jaemtland or Vatterbotten)	0.080	0.070	0.090	0.079	0.080	0.059
Scottish Highland	0.040	0.049	0.081	0.050	0.046	0.048
Sicilian	0.057	0.052	0.087	0.055	0.062	0.056
Småland	0.060	0.056	0.057	0.067	0.062	0.048
South Devon	0.047	0.041	0.047	0.055	0.048	0.043
Spanish Fighting Cattle	0.044	0.050	0.086	0.053	0.062	0.045
Buchara Grey	0.121	0.110	0.078	0.119	0.117	0.117
Hungarian Grey	0.030	0.035	0.063	0.045	0.043	0.035
Hungarian Grey X Bern Red Pied	0.048	0.059	0.086	0.061	0.064	0.066
Sudeten	0.042	0.036	0.066	0.045	0.046	0.038
Sudeten X Simmental	0.051	0.051	0.090	0.060	0.060	0.045
Sudeten X Tesstal?	0.042	0.040	0.070	0.052	0.048	0.046
Tarentaise	0.041	0.045	0.080	0.049	0.055	0.033
Telemark	0.045	0.041	0.055	0.053	0.039	0.034
Tudanca	0.050	0.037	0.054	0.050	0.048	0.045
Tuxer	0.068	0.078	0.119	0.071	0.082	0.079
Heck	0.036	0.042	0.061	0.052	0.039	0.037
Niata	0.192	0.207	0.246	0.199	0.203	0.205
Veredelter Landschlag	0.050	0.045	0.064	0.060	0.061	0.044
Vogtlaender	0.034	0.041	0.081	0.048	0.044	0.036
Waldviertler X Scheinfelder	0.040	0.042	0.072	0.044	0.058	0.037
Watussi	0.056	0.051	0.061	0.062	0.063	0.045
Zebu	0.071	0.062	0.054	0.076	0.072	0.061
Zebu (Africa)	0.065	0.065	0.064	0.081	0.069	0.057
Zebu (Asian)	0.056	0.057	0.074	0.069	0.061	0.057
Zebu (Indian)	0.066	0.056	0.052	0.072	0.065	0.059
Zillertaler	0.040	0.049	0.090	0.052	0.050	0.048

	Haná-Berne	Iceland	Jersey	Jersey (polled)	Jutland	Kampeten: Styrian Bergscheck
Ayrshire	0.055	0.033	0.049	0.047	0.053	0.035
Blondvieh: Carinthian	0.031	0.049	0.067	0.063	0.036	0.031
Blondvieh: Lavanttaler	0.036	0.054	0.067	0.065	0.039	0.029
Blondvieh: Mariahofer	0.056	0.055	0.051	0.048	0.062	0.035
Blondvieh: Murbodner	0.034	0.049	0.065	0.059	0.044	0.032
Blondvieh: Waldviertler	0.031	0.045	0.067	0.064	0.031	0.029
Bos primigenius (Aurochs)	0.051	0.075	0.100	0.094	0.056	0.056
Brazilian	0.052	0.061	0.072	0.067	0.061	0.045
Montafon	0.031	0.052	0.071	0.064	0.036	0.029
Buša	0.047	0.045	0.066	0.062	0.037	0.034

Chianina	0.044	0.065	0.080	0.076	0.042	0.050
Chillingham	0.076	0.058	0.077	0.074	0.067	0.056
Devon	0.049	0.041	0.049	0.048	0.051	0.034
Egerlaender	0.042	0.071	0.080	0.079	0.054	0.048
Hérens	0.065	0.042	0.050	0.051	0.068	0.040
Fjällko	0.040	0.041	0.063	0.064	0.031	0.037
Bern Red Pied	0.032	0.052	0.070	0.065	0.040	0.029
Freiburg Red Pied	0.044	0.067	0.076	0.074	0.058	0.049
Simmental	0.047	0.044	0.057	0.053	0.059	0.032
South Moravian Red Pied	0.036	0.051	0.068	0.062	0.047	0.029
Rubia Gallega	0.050	0.078	0.100	0.092	0.053	0.066
Allgaeuer Grey	0.052	0.059	0.067	0.065	0.061	0.038
Krainer Grey	0.047	0.053	0.065	0.060	0.055	0.043
Oberinntaler Grey	0.038	0.039	0.060	0.053	0.046	0.019
Haná-Berne		0.058	0.080	0.076	0.041	0.040
Iceland	0.058		0.054	0.050	0.056	0.041
Jersey	0.080	0.054		0.045	0.081	0.060
Jersey (polled)	0.076	0.050	0.045		0.080	0.054
Jutland	0.041	0.056	0.081	0.080		0.045
Kampeten: Styrian Bergscheck	0.040	0.041	0.060	0.054	0.045	
Kampeten: Welser Schecken	0.040	0.068	0.090	0.080	0.049	0.045
Kerry	0.042	0.036	0.065	0.059	0.035	0.033
Cretan	0.065	0.062	0.069	0.070	0.057	0.057
Kuhlaender	0.030	0.045	0.064	0.060	0.038	0.029
Landschlag von Warnsdorf	0.057	0.053	0.051	0.060	0.063	0.048
Landschlag von Winkelsdorf	0.043	0.070	0.090	0.089	0.045	0.054
Landschlag X Simmental	0.043	0.063	0.078	0.074	0.048	0.045
Limousin	0.055	0.046	0.048	0.046	0.061	0.043
Moravian Landschlag	0.047	0.043	0.056	0.051	0.054	0.035
Normande	0.063	0.056	0.048	0.046	0.065	0.046
North Wales	0.038	0.044	0.062	0.059	0.038	0.034
White Park	0.065	0.045	0.062	0.064	0.060	0.054
Pinzgauer	0.042	0.042	0.052	0.045	0.052	0.029
Pinzgauer X Scottish Highland	0.063	0.073	0.080	0.073	0.070	0.047
Pinzgauer X Simmentaler	0.070	0.058	0.049	0.053	0.078	0.054
Pinzgauer: Moelltaler	0.033	0.055	0.071	0.066	0.043	0.036
Pinzgauer: Pustertaler	0.079	0.081	0.083	0.073	0.088	0.058
Pirenaica	0.050	0.041	0.051	0.047	0.051	0.034
Red Poll	0.079	0.063	0.069	0.061	0.084	0.053
Maas-Rhein-Ijsselschlag	0.042	0.040	0.053	0.050	0.040	0.031
Danish Red	0.040	0.057	0.072	0.071	0.035	0.043
Angeln	0.049	0.043	0.059	0.054	0.051	0.033
Bohemian Red	0.029	0.045	0.063	0.059	0.038	0.027
Polish Red	0.040	0.052	0.073	0.072	0.034	0.042
Sanga	0.063	0.085	0.106	0.101	0.056	0.070
Sardinian	0.051	0.066	0.082	0.078	0.049	0.051
Scheinfelder	0.044	0.058	0.079	0.071	0.052	0.046

Schoenhengster	0.028	0.048	0.070	0.065	0.038	0.030
Holland Black Pied	0.048	0.048	0.064	0.058	0.057	0.034
Andalusian Black	0.035	0.056	0.082	0.075	0.040	0.035
Sweden (Jaemtland or Vatterbotten)	0.069	0.065	0.079	0.083	0.060	0.062
Scottish Highland	0.064	0.052	0.060	0.051	0.071	0.046
Sicilian	0.063	0.072	0.072	0.076	0.074	0.053
Småland	0.047	0.048	0.077	0.076	0.038	0.052
South Devon	0.039	0.052	0.067	0.065	0.037	0.043
Spanish Fighting Cattle	0.067	0.056	0.071	0.064	0.071	0.040
Buchara Grey	0.101	0.126	0.149	0.144	0.091	0.115
Hungarian Grey	0.047	0.049	0.059	0.054	0.056	0.038
Hungarian Grey X Bern Red Pied	0.069	0.072	0.075	0.074	0.082	0.065
Sudeten	0.039	0.049	0.059	0.065	0.045	0.038
Sudeten X Simmental	0.065	0.049	0.043	0.052	0.066	0.046
Sudeten X Tesstal?	0.048	0.053	0.062	0.063	0.057	0.045
Tarentaise	0.056	0.048	0.060	0.056	0.058	0.029
Telemark	0.038	0.040	0.062	0.059	0.034	0.036
Tudanca	0.042	0.060	0.077	0.074	0.037	0.041
Tuxer	0.099	0.085	0.077	0.069	0.106	0.073
Heck	0.046	0.038	0.056	0.055	0.047	0.038
Niata	0.228	0.202	0.174	0.176	0.237	0.204
Veredelter Landschlag	0.044	0.049	0.072	0.070	0.053	0.046
Vogtlaender	0.055	0.046	0.043	0.045	0.065	0.037
Waldviertler X Scheinfelder	0.051	0.048	0.061	0.059	0.053	0.034
Watussi	0.046	0.061	0.080	0.075	0.054	0.047
Zebu	0.056	0.067	0.091	0.087	0.045	0.059
Zebu (Africa)	0.057	0.059	0.089	0.081	0.063	0.061
Zebu (Asian)	0.062	0.061	0.065	0.066	0.063	0.057
Zebu (Indian)	0.052	0.074	0.093	0.086	0.049	0.058
Zillertaler	0.067	0.059	0.055	0.049	0.075	0.045

	Kampeten: Welser Schecken	Kerry	Cretan	Kuhlaender	Landschlag von Warnsdorf	Landschlag von Winkelsdorf
Ayrshire	0.062	0.035	0.064	0.041	0.053	0.069
Blondvieh: Carinthian	0.046	0.033	0.059	0.020	0.047	0.041
Blondvieh: Lavanttaler	0.047	0.038	0.055	0.026	0.052	0.044
Blondvieh: Mariahofer	0.059	0.052	0.057	0.042	0.049	0.066
Blondvieh: Murbodner	0.048	0.038	0.060	0.021	0.045	0.049
Blondvieh: Waldviertler	0.044	0.027	0.049	0.022	0.050	0.042
Bos primigenius (Aurochs)	0.044	0.061	0.077	0.059	0.086	0.063
Brazilian	0.055	0.053	0.057	0.046	0.057	0.064
Montafon	0.042	0.032	0.054	0.023	0.052	0.043
Buša	0.055	0.026	0.041	0.036	0.051	0.052
Chianina	0.049	0.046	0.049	0.040	0.066	0.050
Chillingham	0.074	0.055	0.068	0.066	0.077	0.083
Devon	0.061	0.034	0.049	0.032	0.039	0.061

Egerlaender	0.058	0.055	0.069	0.040	0.057	0.049
Hérens	0.072	0.048	0.067	0.052	0.051	0.080
Fjällko	0.056	0.024	0.054	0.032	0.048	0.047
Bern Red Pied	0.044	0.036	0.060	0.024	0.050	0.043
Freiburg Red Pied	0.052	0.056	0.070	0.044	0.060	0.061
Simmental	0.052	0.043	0.060	0.037	0.047	0.064
South Moravian Red Pied	0.041	0.042	0.061	0.027	0.051	0.048
Rubia Gallega	0.058	0.055	0.065	0.054	0.076	0.056
Allgaeuer Grey	0.055	0.055	0.065	0.044	0.054	0.061
Krainer Grey	0.051	0.047	0.063	0.041	0.057	0.064
Oberinntaler Grey	0.046	0.032	0.063	0.029	0.050	0.057
Haná-Berne	0.040	0.042	0.065	0.030	0.057	0.043
Iceland	0.068	0.036	0.062	0.045	0.053	0.070
Jersey	0.090	0.065	0.069	0.064	0.051	0.090
Jersey (polled)	0.080	0.059	0.070	0.060	0.060	
Jutland	0.049	0.035	0.057	0.038	0.063	0.045
Kampeten: Styrian Bergscheck	0.045	0.033	0.057	0.029	0.048	0.054
Kampeten: Welser Schecken		0.050	0.070	0.044	0.075	0.056
Kerry	0.050		0.052	0.034	0.053	0.054
Cretan	0.070	0.052		0.052	0.059	0.065
Kuhlaender	0.044	0.034	0.052		0.045	0.043
Landschlag von Warnsdorf	0.075	0.053	0.059	0.045		0.067
Landschlag von Winkelsdorf	0.056	0.054	0.065	0.043	0.067	
Landschlag X Simmental	0.058	0.045	0.062	0.034	0.058	0.042
Limousin	0.065	0.048	0.059	0.038	0.045	0.068
Moravian Landschlag	0.054	0.041	0.057	0.031	0.044	0.060
Normande	0.069	0.054	0.067	0.047	0.058	0.074
North Wales	0.049	0.029	0.045	0.024	0.045	0.051
White Park	0.076	0.045	0.052	0.055	0.052	0.074
Pinzgauer	0.051	0.038	0.056	0.027	0.041	0.059
Pinzgauer X Scottish Highland	0.064	0.067	0.086	0.055	0.071	0.075
Pinzgauer X Simmentaler	0.078	0.063	0.074	0.056	0.053	0.088
Pinzgauer: Moelltaler	0.043	0.040	0.050	0.025	0.049	0.046
Pinzgauer: Pustertaler	0.073	0.080	0.087	0.071	0.084	0.094
Pirenaica	0.056	0.037	0.051	0.035	0.047	0.061
Red Poll	0.074	0.067	0.079	0.068	0.068	0.089
Maas-Rhein-Ijsselschlag	0.054	0.029	0.046	0.025	0.043	0.053
Danish Red	0.055	0.038	0.057	0.034	0.056	0.043
Angeln	0.053	0.033	0.052	0.037	0.049	0.061
Bohemian Red	0.044	0.030	0.053	0.018	0.043	0.041
Polish Red	0.054	0.033	0.044	0.029	0.052	0.040
Sanga	0.075	0.066	0.067	0.064	0.083	0.054
Sardinian	0.062	0.054	0.065	0.044	0.069	0.051
Scheinfelder	0.054	0.044	0.053	0.040	0.056	0.055
Schoenhengster	0.042	0.033	0.057	0.020	0.048	0.042
Holland Black Pied	0.047	0.044	0.062	0.042	0.056	0.063
Andalusian Black	0.040	0.035	0.056	0.037	0.061	0.046

Sweden (Jaemtland or Vatterbotten)	0.082	0.058	0.086	0.063	0.074	0.073
Scottish Highland	0.066	0.054	0.071	0.054	0.057	0.082
Sicilian	0.071	0.070	0.086	0.057	0.064	0.075
Småland	0.062	0.032	0.055	0.043	0.064	0.055
South Devon	0.056	0.033	0.049	0.029	0.049	0.045
Spanish Fighting Cattle	0.060	0.053	0.076	0.059	0.069	0.080
Buchara Grey	0.100	0.104	0.094	0.102	0.125	0.091
Hungarian Grey	0.055	0.044	0.058	0.035	0.048	0.061
Hungarian Grey X Bern Red Pied	0.070	0.070	0.077	0.063	0.067	0.084
Sudeten	0.057	0.042	0.058	0.030	0.045	0.049
Sudeten X Simmental	0.076	0.053	0.070	0.050	0.052	0.072
Sudeten X Tesstal?	0.059	0.048	0.065	0.042	0.046	0.064
Tarentaise	0.058	0.045	0.065	0.044	0.060	0.068
Telemark	0.048	0.024	0.051	0.030	0.051	0.054
Tudanca	0.045	0.043	0.051	0.036	0.057	0.047
Tuxer	0.093	0.092	0.097	0.086	0.085	0.109
Heck	0.056	0.032	0.049	0.036	0.044	0.063
Niata	0.227	0.219	0.216	0.214	0.198	0.241
Veredelter Landschlag	0.060	0.046	0.061	0.037	0.056	0.052
Vogtlaender	0.067	0.051	0.069	0.040	0.043	0.070
Waldviertler X Scheinfelder	0.062	0.043	0.060	0.037	0.047	0.057
Watussi	0.062	0.050	0.073	0.044	0.060	0.057
Zebu	0.066	0.048	0.052	0.051	0.070	0.051
Zebu (Africa)	0.069	0.051	0.068	0.056	0.072	0.070
Zebu (Asian)	0.067	0.058	0.056	0.048	0.063	0.072
Zebu (Indian)	0.056	0.053	0.054	0.047	0.071	0.053
Zillertaler	0.067	0.062	0.072	0.054	0.062	0.083
	Landschlag X Simmental	Limousin	Moravian Landschlag	Normande	North Wales	White Park
Ayrshire	0.057	0.040	0.043	0.040	0.040	0.055
Blondvieh: Carinthian	0.034	0.040	0.036	0.046	0.027	0.059
Blondvieh: Lavanttaler	0.037	0.045	0.043	0.044	0.033	0.059
Blondvieh: Mariahofer	0.056	0.040	0.042	0.038	0.043	0.058
Blondvieh: Murbodner	0.035	0.035	0.034	0.046	0.028	0.062
Blondvieh: Waldviertler	0.040	0.048	0.038	0.053	0.025	0.050
Bos primigenius (Aurochs)	0.068	0.079	0.070	0.084	0.062	0.084
Brazilian	0.057	0.045	0.049	0.057	0.041	0.070
Montafon	0.033	0.044	0.039	0.050	0.027	0.058
Buša	0.045	0.054	0.045	0.060	0.035	0.041
Chianina	0.052	0.059	0.055	0.061	0.039	0.068
Chillingham	0.074	0.075	0.067	0.077	0.058	0.060
Devon	0.047	0.029	0.036	0.036	0.027	0.047
Egerlaender	0.040	0.056	0.056	0.058	0.049	0.071
Hérens	0.067	0.050	0.049	0.053	0.049	0.051
Fjällko	0.044	0.049	0.044	0.053	0.035	0.045
Bern Red Pied	0.034	0.043	0.041	0.048	0.030	0.061

Freiburg Red Pied	0.059	0.050	0.051	0.059	0.044	0.076
Simmental	0.054	0.034	0.035	0.046	0.035	0.057
South Moravian Red Pied	0.043	0.042	0.036	0.047	0.035	0.064
Rubia Gallega	0.053	0.073	0.067	0.083	0.050	0.078
Allgaeuer Grey	0.060	0.050	0.043	0.058	0.047	0.066
Krainer Grey	0.058	0.049	0.046	0.054	0.040	0.069
Oberinntaler Grey	0.044	0.041	0.035	0.046	0.034	0.057
Haná-Berne	0.043	0.055	0.047	0.063	0.038	0.065
Iceland	0.063	0.046	0.043	0.056	0.044	0.045
Jersey	0.078	0.048	0.056	0.048	0.062	0.062
Jersey (polled)	0.074	0.046	0.051	0.046	0.059	0.064
Jutland	0.048	0.061	0.054	0.065	0.038	0.060
Kampeten: Styrian Bergscheck	0.045	0.043	0.035	0.046	0.034	0.054
Kampeten: Welser Schecken	0.058	0.065	0.054	0.069	0.049	0.076
Kerry	0.045	0.048	0.041	0.054	0.029	0.045
Cretan	0.062	0.059	0.057	0.067	0.045	0.052
Kuhlaender	0.034	0.038	0.031	0.047	0.024	0.055
Landschlag von Warnsdorf	0.058	0.045	0.044	0.058	0.045	0.052
Landschlag von Winkelsdorf	0.042	0.068	0.060	0.074	0.051	0.074
Landschlag X Simmental		0.055	0.050	0.060	0.040	0.069
Limousin	0.055		0.035	0.034	0.037	0.061
Moravian Landschlag	0.050	0.035		0.050	0.036	0.055
Normande	0.060	0.034	0.050		0.047	0.067
North Wales	0.040	0.037	0.036	0.047		0.050
White Park	0.069	0.061	0.055	0.067	0.050	
Pinzgauer	0.046	0.027	0.028	0.038	0.028	0.057
Pinzgauer X Scottish Highland	0.060	0.062	0.061	0.058	0.063	0.083
Pinzgauer X Simmentaler	0.073	0.044	0.050	0.053	0.053	0.068
Pinzgauer: Moelltaler	0.039	0.042	0.039	0.052	0.026	0.061
Pinzgauer: Pustertaler	0.082	0.073	0.072	0.069	0.073	0.090
Pirenaica	0.053	0.034	0.036	0.037	0.030	0.054
Red Poll	0.081	0.066	0.060	0.068	0.067	0.075
Maas-Rhein-Ijsselschlag	0.044	0.032	0.032	0.038	0.024	0.044
Danish Red	0.039	0.052	0.050	0.052	0.037	0.058
Angeln	0.049	0.046	0.040	0.052	0.035	0.050
Bohemian Red	0.035	0.040	0.032	0.048	0.028	0.052
Polish Red	0.035	0.055	0.044	0.062	0.033	0.050
Sanga	0.060	0.087	0.081	0.088	0.064	0.075
Sardinian	0.047	0.058	0.061	0.056	0.047	0.072
Scheinfelder	0.047	0.054	0.050	0.064	0.038	0.054
Schoenhengster	0.035	0.045	0.035	0.053	0.029	0.056
Holland Black Pied	0.061	0.047	0.039	0.051	0.043	0.060
Andalusian Black	0.043	0.055	0.049	0.063	0.035	0.059
Sweden (Jaemtland or Vatterbotten)	0.069	0.074	0.072	0.070	0.070	0.068
Scottish Highland	0.071	0.049	0.047	0.057	0.049	0.068
Sicilian	0.070	0.060	0.059	0.062	0.065	0.084

Småland	0.050	0.062	0.055	0.069	0.041	0.049
South Devon	0.040	0.044	0.042	0.050	0.027	0.054
Spanish Fighting Cattle	0.070	0.059	0.055	0.061	0.057	0.070
Buchara Grey	0.098	0.124	0.115	0.131	0.099	0.116
Hungarian Grey	0.050	0.029	0.037	0.042	0.030	0.064
Hungarian Grey X Bern Red Pied	0.081	0.052	0.058	0.067	0.061	0.083
Sudeten	0.049	0.045	0.036	0.053	0.037	0.055
Sudeten X Simmental	0.061	0.047	0.052	0.040	0.052	0.057
Sudeten X Tesstal?	0.057	0.042	0.039	0.052	0.042	0.063
Tarentaise	0.056	0.051	0.046	0.051	0.047	0.058
Telemark	0.047	0.047	0.041	0.052	0.026	0.047
Tudanca	0.048	0.056	0.049	0.061	0.037	0.064
Tuxer	0.100	0.076	0.075	0.077	0.086	0.095
Heck	0.055	0.041	0.040	0.052	0.025	0.046
Niata	0.226	0.190	0.199	0.190	0.211	0.215
Veredelter Landschlag	0.048	0.049	0.043	0.062	0.041	0.059
Vogtlaender	0.058	0.029	0.036	0.035	0.043	0.063
Waldviertler X Scheinfelder	0.050	0.041	0.042	0.046	0.036	0.050
Watussi	0.050	0.056	0.053	0.062	0.050	0.066
Zebu	0.052	0.072	0.065	0.076	0.051	0.058
Zebu (Africa)	0.060	0.065	0.062	0.079	0.056	0.068
Zebu (Asian)	0.063	0.046	0.053	0.052	0.049	0.068
Zebu (Indian)	0.049	0.069	0.062	0.071	0.049	0.069
Zillertaler	0.072	0.047	0.051	0.047	0.054	0.072

	Pinzgauer	Pinzgauer X Scottish Highland	Pinzgauer X Simmental	Pinzgauer: Moelltaler	Pinzgauer: Pustertaler	Pirenaica
Ayrshire	0.035	0.059	0.051	0.051	0.072	0.033
Blondvieh: Carinthian	0.029	0.054	0.062	0.027	0.075	0.035
Blondvieh: Lavanttaler	0.036	0.051	0.063	0.032	0.071	0.039
Blondvieh: Mariahofer	0.037	0.053	0.053	0.045	0.059	0.036
Blondvieh: Murbodner	0.024	0.048	0.053	0.027	0.072	0.038
Blondvieh: Waldviertler	0.034	0.061	0.061	0.030	0.075	0.036
Bos primigenius (Aurochs)	0.067	0.074	0.089	0.060	0.084	0.071
Brazilian	0.042	0.065	0.061	0.040	0.068	0.043
Montafon	0.031	0.053	0.063	0.024	0.071	0.038
Buša	0.044	0.065	0.067	0.042	0.078	0.042
Chianina	0.046	0.075	0.073	0.035	0.082	0.049
Chillingham	0.065	0.078	0.075	0.069	0.078	0.061
Devon	0.025	0.060	0.047	0.035	0.073	0.030
Egerlaender	0.050	0.056	0.074	0.042	0.083	0.057
Hérens	0.044	0.062	0.045	0.060	0.066	0.045
Fjällko	0.041	0.066	0.068	0.041	0.084	0.042
Bern Red Pied	0.031	0.050	0.061	0.025	0.072	0.040
Freiburg Red Pied	0.039	0.066	0.059	0.039	0.079	0.050
Simmental	0.027	0.061	0.047	0.037	0.062	0.033
South Moravian Red Pied	0.031	0.052	0.061	0.031	0.066	0.035

Rubia Gallega	0.064	0.086	0.089	0.049	0.102	0.067
Allgaeuer Grey	0.041	0.057	0.059	0.045	0.063	0.047
Krainer Grey	0.035	0.064	0.057	0.043	0.072	0.040
Oberinntaler Grey	0.026	0.049	0.052	0.037	0.062	0.036
Haná-Berne	0.042	0.063	0.070	0.033	0.079	0.050
Iceland	0.042	0.073	0.058	0.055	0.081	0.041
Jersey	0.052	0.080	0.049	0.071	0.083	0.051
Jersey (polled)	0.045	0.073	0.053	0.066	0.073	0.047
Jutland	0.052	0.070	0.078	0.043	0.088	0.051
Kampeten: Styrian Bergscheck	0.029	0.047	0.054	0.036	0.058	0.034
Kampeten: Welser Schecken	0.051	0.064	0.078	0.043	0.073	0.056
Kerry	0.038	0.067	0.063	0.040	0.080	0.037
Cretan	0.056	0.086	0.074	0.050	0.087	0.051
Kuhlaender	0.027	0.055	0.056	0.025	0.071	0.035
Landschlag von Warnsdorf	0.041	0.071	0.053	0.049	0.084	0.047
Landschlag von Winkelsdorf	0.059	0.075	0.088	0.046	0.094	0.061
Landschlag X Simmental	0.046	0.060	0.073	0.039	0.082	0.053
Limousin	0.027	0.062	0.044	0.042	0.073	0.034
Moravian Landschlag	0.028	0.061	0.050	0.039	0.072	0.036
Normande	0.038	0.058	0.053	0.052	0.069	0.037
North Wales	0.028	0.063	0.053	0.026	0.073	0.030
White Park	0.057	0.083	0.068	0.061	0.090	0.054
Pinzgauer		0.053	0.041	0.031	0.064	0.029
Pinzgauer X Scottish Highland	0.053		0.067	0.059	0.062	0.063
Pinzgauer X Simmentaler	0.041	0.067		0.061	0.071	0.054
Pinzgauer: Moelltaler	0.031	0.059	0.061		0.073	0.039
Pinzgauer: Pustertaler	0.064	0.062	0.071	0.073		0.069
Pirenaica	0.029	0.063	0.054	0.039	0.069	
Red Poll	0.059	0.071	0.070	0.068	0.066	0.056
Maas-Rhein-Ijsselschlag	0.028	0.058	0.051	0.034	0.072	0.030
Danish Red	0.046	0.061	0.073	0.040	0.086	0.045
Angeln	0.035	0.061	0.052	0.041	0.071	0.041
Bohemian Red	0.028	0.055	0.058	0.028	0.075	0.036
Polish Red	0.047	0.071	0.073	0.035	0.085	0.046
Sanga	0.078	0.086	0.105	0.063	0.105	0.076
Sardinian	0.052	0.067	0.079	0.047	0.085	0.052
Scheinfelder	0.048	0.071	0.069	0.040	0.084	0.053
Schoenhengster	0.031	0.056	0.061	0.027	0.075	0.040
Holland Black Pied	0.039	0.059	0.060	0.043	0.065	0.038
Andalusian Black	0.045	0.062	0.073	0.034	0.076	0.046
Sweden (Jaemtland or Vatterbot-ten)	0.070	0.073	0.086	0.075	0.104	0.072
Scottish Highland	0.040	0.062	0.048	0.055	0.065	0.043
Sicilian	0.053	0.058	0.065	0.062	0.078	0.064
Småland	0.055	0.080	0.077	0.052	0.094	0.053
South Devon	0.036	0.068	0.065	0.030	0.085	0.040
Spanish Fighting Cattle	0.052	0.062	0.065	0.062	0.062	0.050

Buchara Grey	0.118	0.129	0.141	0.093	0.145	0.115
Hungarian Grey	0.026	0.059	0.049	0.033	0.069	0.034
Hungarian Grey X Bern Red Pied	0.056	0.083	0.065	0.060	0.082	0.058
Sudeten	0.036	0.062	0.058	0.040	0.078	0.039
Sudeten X Simmental	0.045	0.064	0.055	0.060	0.077	0.045
Sudeten X Tesstal?	0.038	0.067	0.061	0.040	0.083	0.042
Tarentaise	0.043	0.055	0.056	0.052	0.061	0.042
Telemark	0.035	0.064	0.056	0.037	0.077	0.037
Tudanca	0.044	0.063	0.072	0.030	0.076	0.045
Tuxer	0.072	0.078	0.068	0.088	0.064	0.076
Heck	0.032	0.067	0.051	0.038	0.075	0.029
Niata	0.195	0.204	0.174	0.215	0.185	0.199
Veredelter Landschlag	0.046	0.070	0.065	0.046	0.084	0.052
Vogtlaender	0.027	0.055	0.038	0.050	0.066	0.035
Waldviertler X Scheinfelder	0.039	0.059	0.055	0.044	0.070	0.039
Watussi	0.051	0.063	0.073	0.047	0.090	0.056
Zebu	0.065	0.083	0.092	0.052	0.100	0.063
Zebu (Africa)	0.063	0.085	0.081	0.060	0.098	0.067
Zebu (Asian)	0.049	0.075	0.064	0.051	0.082	0.050
Zebu (Indian)	0.060	0.078	0.087	0.043	0.093	0.060
Zillertaler	0.041	0.060	0.044	0.058	0.049	0.044

	Red Poll	Maas- Rhein- Ijsselschlag	Danish Red	Angeln	Bohemian Red	Polish Red
Ayrshire	0.063	0.033	0.049	0.043	0.041	0.053
Blondvieh: Carinthian	0.070	0.027	0.028	0.041	0.019	0.033
Blondvieh: Lavanttaler	0.070	0.031	0.030	0.040	0.024	0.036
Blondvieh: Mariahofer	0.053	0.037	0.051	0.045	0.043	0.055
Blondvieh: Murbodner	0.069	0.030	0.038	0.038	0.023	0.039
Blondvieh: Waldviertler	0.070	0.027	0.030	0.038	0.020	0.027
Bos primigenius (Aurochs)	0.083	0.066	0.068	0.059	0.059	0.065
Brazilian	0.058	0.048	0.062	0.045	0.049	0.058
Montafon	0.069	0.029	0.033	0.037	0.022	0.032
Buša	0.070	0.031	0.039	0.036	0.032	0.028
Chianina	0.082	0.043	0.049	0.051	0.042	0.043
Chillingham	0.066	0.063	0.072	0.055	0.067	0.065
Devon	0.062	0.024	0.043	0.037	0.034	0.043
Egerlaender	0.086	0.047	0.039	0.057	0.037	0.049
Hérens	0.055	0.046	0.065	0.040	0.051	0.063
Fjällko	0.075	0.026	0.029	0.042	0.027	0.030
Bern Red Pied	0.069	0.031	0.032	0.040	0.022	0.038
Freiburg Red Pied	0.077	0.049	0.056	0.054	0.044	0.061
Simmental	0.053	0.037	0.057	0.035	0.037	0.053
South Moravian Red Pied	0.059	0.036	0.044	0.039	0.027	0.042
Rubia Gallega	0.098	0.060	0.057	0.065	0.054	0.051
Allgaeuer Grey	0.055	0.046	0.056	0.045	0.044	0.058
Krainer Grey	0.069	0.043	0.055	0.048	0.042	0.056

Oberinntaler Grey	0.060	0.032	0.043	0.035	0.026	0.044
Haná-Berne	0.079	0.042	0.040	0.049	0.029	0.040
Iceland	0.063	0.040	0.057	0.043	0.045	0.052
Jersey	0.069	0.053	0.072	0.059	0.063	0.073
Jersey (polled)	0.061	0.050	0.071	0.054	0.059	0.072
Jutland	0.084	0.040	0.035	0.051	0.038	0.034
Kampeten: Styrian Bergscheck	0.053	0.031	0.043	0.033	0.027	0.042
Kampeten: Welser Schecken	0.074	0.054	0.055	0.053	0.044	0.054
Kerry	0.067	0.029	0.038	0.033	0.030	0.033
Cretan	0.079	0.046	0.057	0.052	0.053	0.044
Kuhlaender	0.068	0.025	0.034	0.037	0.018	0.029
Landschlag von Warnsdorf	0.068	0.043	0.056	0.049	0.043	0.052
Landschlag von Winkelsdorf	0.089	0.053	0.043	0.061	0.041	0.040
Landschlag X Simmental	0.081	0.044	0.039	0.049	0.035	0.035
Limousin	0.066	0.032	0.052	0.046	0.040	0.055
Moravian Landschlag	0.060	0.032	0.050	0.040	0.032	0.044
Normande	0.068	0.038	0.052	0.052	0.048	0.062
North Wales	0.067	0.024	0.037	0.035	0.028	0.033
White Park	0.075	0.044	0.058	0.050	0.052	0.050
Pinzgauer	0.059	0.028	0.046	0.035	0.028	0.047
Pinzgauer X Scottish Highland	0.071	0.058	0.061	0.061	0.055	0.071
Pinzgauer X Simmentaler	0.070	0.051	0.073	0.052	0.058	0.073
Pinzgauer: Moelltaler	0.068	0.034	0.040	0.041	0.028	0.035
Pinzgauer: Pustertaler	0.066	0.072	0.086	0.071	0.075	0.085
Pirenaica	0.056	0.030	0.045	0.041	0.036	0.046
Red Poll		0.066	0.081	0.054	0.068	0.078
Maas-Rhein-Ijsselschlag	0.066		0.033	0.033	0.025	0.035
Danish Red	0.081	0.033		0.050	0.030	0.034
Angeln	0.054	0.033	0.050		0.034	0.045
Bohemian Red	0.068	0.025	0.030	0.034		0.030
Polish Red	0.078	0.035	0.034	0.045	0.030	
Sanga	0.104	0.066	0.053	0.076	0.064	0.051
Sardinian	0.088	0.049	0.041	0.064	0.047	0.050
Scheinfelder	0.077	0.042	0.048	0.045	0.038	0.043
Schoenhengster	0.072	0.031	0.035	0.037	0.015	0.032
Holland Black Pied	0.046	0.039	0.054	0.036	0.041	0.054
Andalusian Black	0.071	0.040	0.043	0.042	0.033	0.039
Sweden (Jaemtland or Vatterbotten)	0.097	0.058	0.052	0.069	0.058	0.063
Scottish Highland	0.043	0.052	0.071	0.042	0.055	0.070
Sicilian	0.072	0.062	0.071	0.061	0.057	0.074
Småland	0.088	0.041	0.041	0.050	0.041	0.034
South Devon	0.077	0.027	0.031	0.043	0.029	0.031
Spanish Fighting Cattle	0.042	0.059	0.072	0.045	0.057	0.069
Buchara Grey	0.141	0.109	0.097	0.113	0.105	0.087
Hungarian Grey	0.060	0.035	0.050	0.040	0.037	0.051
Hungarian Grey X Bern Red Pied	0.066	0.064	0.081	0.061	0.066	0.078

Sudeten	0.071	0.032	0.042	0.044	0.029	0.041
Sudeten X Simmental	0.070	0.043	0.053	0.052	0.047	0.059
Sudeten X Tesstal?	0.063	0.042	0.053	0.047	0.041	0.052
Tarentaise	0.055	0.043	0.055	0.040	0.042	0.054
Telemark	0.071	0.025	0.036	0.035	0.030	0.036
Tudanca	0.071	0.040	0.044	0.047	0.038	0.038
Tuxer	0.053	0.083	0.103	0.074	0.088	0.102
Heck	0.061	0.033	0.048	0.036	0.036	0.044
Niata	0.179	0.208	0.230	0.202	0.215	0.230
Veredelter Landschlag	0.080	0.043	0.050	0.052	0.038	0.039
Vogtlaender	0.061	0.038	0.056	0.046	0.041	0.060
Waldviertler X Scheinfelder	0.065	0.033	0.043	0.045	0.038	0.047
Watussi	0.084	0.047	0.045	0.058	0.041	0.049
Zebu	0.096	0.052	0.044	0.063	0.050	0.033
Zebu (Africa)	0.095	0.058	0.063	0.061	0.053	0.053
Zebu (Asian)	0.085	0.047	0.059	0.062	0.054	0.055
Zebu (Indian)	0.092	0.054	0.048	0.062	0.050	0.039
Zillertaler	0.054	0.051	0.072	0.050	0.057	0.072
	Sanga	Sardinian	Scheinfelder	Schoenhengs-ter	Holland Black Pied	Andalusian Black
Ayrshire	0.083	0.057	0.059	0.047	0.046	0.053
Blondvieh: Carinthian	0.061	0.042	0.043	0.022	0.043	0.035
Blondvieh: Lavanttaler	0.060	0.041	0.043	0.025	0.045	0.034
Blondvieh: Mariahofer	0.080	0.060	0.056	0.047	0.041	0.053
Blondvieh: Murbodner	0.068	0.047	0.043	0.025	0.045	0.039
Blondvieh: Waldviertler	0.059	0.046	0.042	0.023	0.043	0.033
Bos primigenius (Aurochs)	0.074	0.070	0.061	0.057	0.061	0.044
Brazilian	0.078	0.061	0.050	0.049	0.044	0.044
Montafon	0.058	0.043	0.040	0.020	0.043	0.028
Buša	0.058	0.055	0.043	0.035	0.049	0.037
Chianina	0.062	0.051	0.051	0.042	0.057	0.044
Chillingham	0.086	0.081	0.073	0.067	0.061	0.064
Devon	0.072	0.051	0.046	0.039	0.044	0.045
Egerlaender	0.062	0.049	0.051	0.038	0.061	0.046
Hérens	0.093	0.076	0.064	0.053	0.046	0.061
Fjällko	0.061	0.051	0.047	0.032	0.049	0.041
Bern Red Pied	0.062	0.044	0.040	0.021	0.044	0.032
Freiburg Red Pied	0.081	0.062	0.056	0.044	0.052	0.050
Simmental	0.084	0.062	0.048	0.037	0.034	0.043
South Moravian Red Pied	0.072	0.052	0.048	0.028	0.034	0.038
Rubia Gallega	0.058	0.059	0.050	0.052	0.074	0.047
Allgaeuer Grey	0.082	0.066	0.058	0.046	0.041	0.052
Krainer Grey	0.081	0.058	0.056	0.042	0.047	0.051
Oberinntaler Grey	0.073	0.052	0.047	0.029	0.038	0.039
Haná-Berne	0.063	0.051	0.044	0.028	0.048	0.035
Iceland	0.085	0.066	0.058	0.048	0.048	0.056
Jersey	0.106	0.082	0.079	0.070	0.064	0.082

Jersey (polled)	0.101	0.078	0.071	0.065	0.058	0.075
Jutland	0.056	0.049	0.052	0.038	0.057	0.040
Kampeten: Styrian Bergscheck	0.070	0.051	0.046	0.030	0.034	0.035
Kampeten: Welser Schecken	0.075	0.062	0.054	0.042	0.047	0.040
Kerry	0.066	0.054	0.044	0.033	0.044	0.035
Cretan	0.067	0.065	0.053	0.057	0.062	0.056
Kuhlaender	0.064	0.044	0.040	0.020	0.042	0.037
Landschlag von Warnsdorf	0.083	0.069	0.056	0.048	0.056	0.061
Landschlag von Winkelsdorf	0.054	0.051	0.055	0.042	0.063	0.046
Landschlag X Simmental	0.060	0.047	0.047	0.035	0.061	0.043
Limousin	0.087	0.058	0.054	0.045	0.047	0.055
Moravian Landschlag	0.081	0.061	0.050	0.035	0.039	0.049
Normande	0.088	0.056	0.064	0.053	0.051	0.063
North Wales	0.064	0.047	0.038	0.029	0.043	0.035
White Park	0.075	0.072	0.054	0.056	0.060	0.059
Pinzgauer	0.078	0.052	0.048	0.031	0.039	0.045
Pinzgauer X Scottish Highland	0.086	0.067	0.071	0.056	0.059	0.062
Pinzgauer X Simmentaler	0.105	0.079	0.069	0.061	0.060	0.073
Pinzgauer: Moelltaler	0.063	0.047	0.040	0.027	0.043	0.034
Pinzgauer: Pustertaler	0.105	0.085	0.084	0.075	0.065	0.076
Pirenaica	0.076	0.052	0.053	0.040	0.038	0.046
Red Poll	0.104	0.088	0.077	0.072	0.046	0.071
Maas-Rhein-Ijsselschlag	0.066	0.049	0.042	0.031	0.039	0.040
Danish Red	0.053	0.041	0.048	0.035	0.054	0.043
Angeln	0.076	0.064	0.045	0.037	0.036	0.042
Bohemian Red	0.064	0.047	0.038	0.015	0.041	0.033
Polish Red	0.051	0.050	0.043	0.032	0.054	0.039
Sanga		0.055	0.060	0.064	0.082	0.056
Sardinian	0.055		0.053	0.048	0.068	0.048
Scheinfelder	0.060	0.053		0.039	0.056	0.034
Schoenhengster	0.064	0.048	0.039		0.043	0.032
Holland Black Pied	0.082	0.068	0.056	0.043		0.046
Andalusian Black	0.056	0.048	0.034	0.032	0.046	
Sweden (Jaemtland or Vatterbotten)	0.079	0.072	0.077	0.063	0.075	0.072
Scottish Highland	0.099	0.078	0.067	0.056	0.042	0.062
Sicilian	0.096	0.072	0.074	0.059	0.062	0.068
Småland	0.060	0.058	0.048	0.043	0.062	0.045
South Devon	0.057	0.044	0.043	0.032	0.051	0.040
Spanish Fighting Cattle	0.094	0.076	0.065	0.058	0.041	0.052
Buchara Grey	0.076	0.100	0.097	0.102	0.118	0.094
Hungarian Grey	0.078	0.054	0.048	0.039	0.041	0.046
Hungarian Grey X Bern Red Pied	0.105	0.083	0.074	0.069	0.053	0.068
Sudeten	0.071	0.058	0.054	0.034	0.045	0.047
Sudeten X Simmental	0.089	0.066	0.066	0.054	0.055	0.067
Sudeten X Tesstal?	0.082	0.063	0.055	0.043	0.043	0.052
Tarentaise	0.082	0.062	0.058	0.045	0.043	0.049

Telemark	0.067	0.052	0.046	0.032	0.044	0.041
Tudanca	0.060	0.053	0.051	0.038	0.047	0.039
Tuxer	0.127	0.105	0.097	0.089	0.067	0.093
Heck	0.074	0.058	0.048	0.041	0.042	0.044
Niata	0.258	0.231	0.222	0.218	0.198	0.227
Veredelter Landschlag	0.069	0.057	0.048	0.041	0.057	0.048
Vogtlaender	0.091	0.062	0.061	0.045	0.045	0.059
Waldviertler X Scheinfelder	0.072	0.053	0.047	0.041	0.045	0.046
Watussi	0.065	0.049	0.048	0.041	0.061	0.045
Zebu	0.039	0.052	0.050	0.050	0.072	0.048
Zebu (Africa)	0.074	0.068	0.050	0.053	0.071	0.053
Zebu (Asian)	0.080	0.059	0.061	0.057	0.063	0.063
Zebu (Indian)	0.049	0.050	0.051	0.048	0.066	0.048
Zillertaler	0.102	0.076	0.072	0.058	0.045	0.067

	Sweden (Jaemtland or Vatterbotten)	Scottish Highland	Sicilian	Småland	South Devon	Spanish Fighting Cattle
Ayrshire	0.058	0.050	0.062	0.053	0.046	0.054
Blondvieh: Carinthian	0.059	0.057	0.058	0.044	0.026	0.059
Blondvieh: Lavanttaler	0.060	0.060	0.058	0.048	0.035	0.057
Blondvieh: Mariahofer	0.075	0.050	0.062	0.066	0.052	0.051
Blondvieh: Murbodner	0.065	0.050	0.052	0.050	0.031	0.058
Blondvieh: Waldviertler	0.060	0.056	0.064	0.036	0.029	0.060
Bos primigenius (Aurochs)	0.086	0.075	0.069	0.068	0.065	0.066
Brazilian	0.091	0.046	0.058	0.067	0.050	0.050
Montafon	0.064	0.054	0.059	0.044	0.028	0.055
Buša	0.059	0.060	0.073	0.036	0.038	0.059
Chianina	0.080	0.068	0.072	0.054	0.036	0.075
Chillingham	0.086	0.063	0.091	0.063	0.071	0.056
Devon	0.066	0.048	0.061	0.052	0.031	0.056
Egerlaender	0.065	0.075	0.064	0.061	0.045	0.075
Hérens	0.072	0.042	0.067	0.064	0.062	0.045
Fjällko	0.045	0.064	0.067	0.033	0.030	0.065
Bern Red Pied	0.062	0.057	0.058	0.048	0.031	0.058
Freiburg Red Pied	0.082	0.060	0.064	0.067	0.048	0.068
Simmental	0.080	0.040	0.057	0.060	0.047	0.044
South Moravian Red Pied	0.070	0.049	0.052	0.056	0.041	0.050
Rubia Gallega	0.090	0.081	0.087	0.057	0.047	0.086
Allgaeuer Grey	0.079	0.050	0.055	0.067	0.055	0.053
Krainer Grey	0.080	0.046	0.062	0.062	0.048	0.062
Oberinntaler Grey	0.059	0.048	0.056	0.048	0.043	0.045
Haná-Berne	0.069	0.064	0.063	0.047	0.039	0.067
Iceland	0.065	0.052	0.072	0.048	0.052	0.056
Jersey	0.079	0.060	0.072	0.077	0.067	0.071
Jersey (polled)	0.083	0.051	0.076	0.076	0.065	0.064
Jutland	0.060	0.071	0.074	0.038	0.037	0.071
Kampeten: Styrian Bergscheck	0.062	0.046	0.053	0.052	0.043	0.040

Kampeten: Welser Schecken	0.082	0.066	0.071	0.062	0.056	0.060
Kerry	0.058	0.054	0.070	0.032	0.033	0.053
Cretan	0.086	0.071	0.086	0.055	0.049	0.076
Kuhlaender	0.063	0.054	0.057	0.043	0.029	0.059
Landschlag von Warnsdorf	0.074	0.057	0.064	0.064	0.049	0.069
Landschlag von Winkelsdorf	0.073	0.082	0.075	0.055	0.045	0.080
Landschlag X Simmental	0.069	0.071	0.070	0.050	0.040	0.070
Limousin	0.074	0.049	0.060	0.062	0.044	0.059
Moravian Landschlag	0.072	0.047	0.059	0.055	0.042	0.055
Normande	0.070	0.057	0.062	0.069	0.050	0.061
North Wales	0.070	0.049	0.065	0.041	0.027	0.057
White Park	0.068	0.068	0.084	0.049	0.054	0.070
Pinzgauer	0.070	0.040	0.053	0.055	0.036	0.052
Pinzgauer X Scottish Highland	0.073	0.062	0.058	0.080	0.068	0.062
Pinzgauer X Simmentaler	0.086	0.048	0.065	0.077	0.065	0.065
Pinzgauer: Moelltaler	0.075	0.055	0.062	0.052	0.030	0.062
Pinzgauer: Pustertaler	0.104	0.065	0.078	0.094	0.085	0.062
Pirenaica	0.072	0.043	0.064	0.053	0.040	0.050
Red Poll	0.097	0.043	0.072	0.088	0.077	0.042
Maas-Rhein-Ijsselschlag	0.058	0.052	0.062	0.041	0.027	0.059
Danish Red	0.052	0.071	0.071	0.041	0.031	0.072
Angeln	0.069	0.042	0.061	0.050	0.043	0.045
Bohemian Red	0.058	0.055	0.057	0.041	0.029	0.057
Polish Red	0.063	0.070	0.074	0.034	0.031	0.069
Sanga	0.079	0.099	0.096	0.060	0.057	0.094
Sardinian	0.072	0.078	0.072	0.058	0.044	0.076
Scheinfelder	0.077	0.067	0.074	0.048	0.043	0.065
Schoenhengster	0.063	0.056	0.059	0.043	0.032	0.058
Holland Black Pied	0.075	0.042	0.062	0.062	0.051	0.041
Andalusian Black	0.072	0.062	0.068	0.045	0.040	0.052
Sweden (Jaemtland or Vatterbotten)		0.089	0.078	0.060	0.064	0.085
Scottish Highland	0.089		0.059	0.076	0.063	0.044
Sicilian	0.078	0.059		0.085	0.065	0.066
Småland	0.060	0.076	0.085		0.041	0.074
South Devon	0.064	0.063	0.065	0.041		0.069
Spanish Fighting Cattle	0.085	0.044	0.066	0.074	0.069	
Buchara Grey	0.128	0.134	0.139	0.097	0.096	0.133
Hungarian Grey	0.077	0.045	0.057	0.059	0.039	0.053
Hungarian Grey X Bern Red Pied	0.103	0.056	0.072	0.087	0.069	0.065
Sudeten	0.062	0.058	0.056	0.049	0.036	0.064
Sudeten X Simmental	0.061	0.062	0.069	0.063	0.057	0.063
Sudeten X Tesstal?	0.076	0.051	0.057	0.064	0.045	0.060
Tarentaise	0.070	0.053	0.065	0.059	0.058	0.041
Telemark	0.059	0.053	0.066	0.037	0.032	0.061
Tudanca	0.072	0.060	0.064	0.053	0.038	0.065
Tuxer	0.116	0.055	0.080	0.112	0.098	0.062

Heck	0.072	0.042	0.066	0.047	0.038	0.054
Niata	0.234	0.178	0.197	0.235	0.222	0.192
Veredelter Landschlag	0.070	0.070	0.073	0.048	0.046	0.067
Vogtlaender	0.072	0.042	0.051	0.067	0.051	0.053
Waldviertler X Scheinfelder	0.064	0.058	0.067	0.053	0.045	0.055
Watussi	0.060	0.075	0.061	0.056	0.043	0.070
Zebu	0.067	0.089	0.091	0.043	0.043	0.084
Zebu (Africa)	0.077	0.082	0.088	0.049	0.057	0.077
Zebu (Asian)	0.081	0.074	0.077	0.064	0.050	0.078
Zebu (Indian)	0.079	0.084	0.086	0.055	0.045	0.081
Zillertaler	0.090	0.036	0.063	0.080	0.067	0.051

	Bucharan Grey	Hungarian Grey	Hungarian Grey X Bern Red Pied	Sudeten	Sudeten X Simmental	Sudeten X Tesstal?
Ayrshire	0.127	0.044	0.067	0.044	0.042	0.051
Blondvieh: Carinthian	0.103	0.036	0.066	0.031	0.049	0.040
Blondvieh: Lavanttaler	0.104	0.042	0.072	0.037	0.047	0.046
Blondvieh: Mariahofer	0.122	0.042	0.066	0.047	0.046	0.048
Blondvieh: Murbodner	0.108	0.031	0.063	0.036	0.052	0.040
Blondvieh: Waldviertler	0.098	0.043	0.070	0.031	0.052	0.047
Bos primigenius (Aurochs)	0.106	0.067	0.080	0.065	0.088	0.071
Brazilian	0.112	0.033	0.048	0.052	0.069	0.048
Montafon	0.098	0.037	0.067	0.037	0.056	0.044
Buša	0.099	0.051	0.077	0.044	0.055	0.055
Chianina	0.092	0.051	0.073	0.048	0.071	0.055
Chillingham	0.117	0.069	0.089	0.069	0.068	0.078
Devon	0.113	0.031	0.059	0.040	0.045	0.040
Egerlaender	0.106	0.054	0.078	0.047	0.064	0.056
Hérens	0.135	0.049	0.068	0.054	0.043	0.058
Fjällko	0.105	0.048	0.076	0.035	0.048	0.048
Bern Red Pied	0.103	0.036	0.067	0.037	0.053	0.043
Freiburg Red Pied	0.112	0.042	0.062	0.046	0.067	0.050
Simmental	0.121	0.030	0.048	0.042	0.051	0.042
South Moravian Red Pied	0.110	0.035	0.059	0.036	0.051	0.040
Rubia Gallega	0.078	0.063	0.086	0.066	0.090	0.070
Allgaeuer Grey	0.119	0.045	0.061	0.045	0.060	0.052
Krainer Grey	0.117	0.043	0.064	0.046	0.060	0.048
Oberinntaler Grey	0.117	0.035	0.066	0.038	0.045	0.046
Haná-Berne	0.101	0.047	0.069	0.039	0.065	0.048
Iceland	0.126	0.049	0.072	0.049	0.049	0.053
Jersey	0.149	0.059	0.075	0.059	0.043	0.062
Jersey (polled)	0.144	0.054	0.074	0.065	0.052	0.063
Jutland	0.091	0.056	0.082	0.045	0.066	0.057
Kampeten: Styrian Bergscheck	0.115	0.038	0.065	0.038	0.046	0.045
Kampeten: Welser Schecken	0.100	0.055	0.070	0.057	0.076	0.059
Kerry	0.104	0.044	0.070	0.042	0.053	0.048

Cretan	0.094	0.058	0.077	0.058	0.070	0.065
Kuhlaender	0.102	0.035	0.063	0.030	0.050	0.042
Landschlag von Warnsdorf	0.125	0.048	0.067	0.045	0.052	0.046
Landschlag von Winkelsdorf	0.091	0.061	0.084	0.049	0.072	0.064
Landschlag X Simmental	0.098	0.050	0.081	0.049	0.061	0.057
Limousin	0.124	0.029	0.052	0.045	0.047	0.042
Moravian Landschlag	0.115	0.037	0.058	0.036	0.052	0.039
Normande	0.131	0.042	0.067	0.053	0.040	0.052
North Wales	0.099	0.030	0.061	0.037	0.052	0.042
White Park	0.116	0.064	0.083	0.055	0.057	0.063
Pinzgauer	0.118	0.026	0.056	0.036	0.045	0.038
Pinzgauer X Scottish Highland	0.129	0.059	0.083	0.062	0.064	0.067
Pinzgauer X Simmentaler	0.141	0.049	0.065	0.058	0.055	0.061
Pinzgauer: Moelltaler	0.093	0.033	0.060	0.040	0.060	0.040
Pinzgauer: Pustertaler	0.145	0.069	0.082	0.078	0.077	0.083
Pirenaica	0.115	0.034	0.058	0.039	0.045	0.042
Red Poll	0.141	0.060	0.066	0.071	0.070	0.063
Maas-Rhein-Ijsselschlag	0.109	0.035	0.064	0.032	0.043	0.042
Danish Red	0.097	0.050	0.081	0.042	0.053	0.053
Angeln	0.113	0.040	0.061	0.044	0.052	0.047
Bohemian Red	0.105	0.037	0.066	0.029	0.047	0.041
Polish Red	0.087	0.051	0.078	0.041	0.059	0.052
Sanga	0.076	0.078	0.105	0.071	0.089	0.082
Sardinian	0.100	0.054	0.083	0.058	0.066	0.063
Scheinfelder	0.097	0.048	0.074	0.054	0.066	0.055
Schoenhengster	0.102	0.039	0.069	0.034	0.054	0.043
Holland Black Pied	0.118	0.041	0.053	0.045	0.055	0.043
Andalusian Black	0.094	0.046	0.068	0.047	0.067	0.052
Sweden (Jaemtland or Vatterbotten)	0.128	0.077	0.103	0.062	0.061	0.076
Scottish Highland	0.134	0.045	0.056	0.058	0.062	0.051
Sicilian	0.139	0.057	0.072	0.056	0.069	0.057
Småland	0.097	0.059	0.087	0.049	0.063	0.064
South Devon	0.096	0.039	0.069	0.036	0.057	0.045
Spanish Fighting Cattle	0.133	0.053	0.065	0.064	0.063	0.060
Buchara Grey		0.115	0.134	0.113	0.134	0.117
Hungarian Grey	0.115		0.048	0.044	0.053	0.042
Hungarian Grey X Bern Red Pied	0.134	0.048		0.065	0.078	0.059
Sudeten	0.113	0.044	0.065		0.050	0.045
Sudeten X Simmental	0.134	0.053	0.078	0.050		0.058
Sudeten X Tesstal?	0.117	0.042	0.059	0.045	0.058	
Tarentaise	0.125	0.050	0.071	0.050	0.048	0.058
Telemark	0.104	0.043	0.071	0.038	0.052	0.046
Tudanca	0.092	0.046	0.070	0.042	0.066	0.049
Tuxer	0.163	0.075	0.078	0.089	0.081	0.083
Heck	0.110	0.037	0.058	0.040	0.052	0.043
Niata	0.292	0.196	0.188	0.212	0.193	0.203

Veredelter Landschlag	0.106	0.047	0.073	0.046	0.058	0.056
Vogtlaender	0.136	0.036	0.056	0.041	0.039	0.044
Waldviertler X Scheinfelder	0.116	0.041	0.069	0.045	0.046	0.052
Watussi	0.108	0.053	0.080	0.053	0.065	0.055
Zebu	0.076	0.067	0.095	0.060	0.074	0.071
Zebu (Africa)	0.107	0.061	0.085	0.068	0.077	0.072
Zebu (Asian)	0.112	0.050	0.069	0.057	0.063	0.061
Zebu (Indian)	0.075	0.061	0.086	0.061	0.077	0.065
Zillertaler	0.140	0.049	0.060	0.058	0.055	0.058
	Tarentaise	Telemark	Tudanca	Tuxer	Heck	Niata
Ayrshire	0.043	0.036	0.054	0.081	0.037	0.200
Blondvieh: Carinthian	0.047	0.034	0.037	0.090	0.040	0.218
Blondvieh: Lavanttaler	0.041	0.037	0.040	0.088	0.044	0.217
Blondvieh: Mariahofer	0.041	0.050	0.052	0.067	0.048	0.192
Blondvieh: Murbodner	0.048	0.035	0.040	0.085	0.038	0.210
Blondvieh: Waldviertler	0.044	0.024	0.034	0.090	0.034	0.221
Bos primigenius (Aurochs)	0.068	0.059	0.055	0.102	0.065	0.236
Brazilian	0.056	0.054	0.046	0.076	0.044	0.199
Montafon	0.046	0.034	0.033	0.088	0.039	0.218
Buša	0.045	0.031	0.042	0.092	0.039	0.221
Chianina	0.063	0.040	0.036	0.099	0.047	0.226
Chillingham	0.054	0.060	0.068	0.084	0.055	0.210
Devon	0.047	0.034	0.046	0.079	0.031	0.200
Egerlaender	0.061	0.054	0.052	0.102	0.059	0.226
Hérens	0.041	0.050	0.064	0.064	0.044	0.183
Fjällko	0.051	0.027	0.040	0.097	0.040	0.224
Bern Red Pied	0.046	0.036	0.037	0.088	0.042	0.217
Freiburg Red Pied	0.061	0.051	0.049	0.089	0.048	0.210
Simmental	0.041	0.045	0.050	0.068	0.036	0.192
South Moravian Red Pied	0.045	0.041	0.037	0.078	0.042	0.207
Rubia Gallega	0.080	0.055	0.054	0.119	0.061	0.246
Allgaeuer Grey	0.049	0.053	0.050	0.071	0.052	0.199
Krainer Grey	0.055	0.039	0.048	0.082	0.039	0.203
Oberinntaler Grey	0.033	0.034	0.045	0.079	0.037	0.205
Haná-Berne	0.056	0.038	0.042	0.099	0.046	0.228
Iceland	0.048	0.040	0.060	0.085	0.038	0.202
Jersey	0.060	0.062	0.077	0.077	0.056	0.174
Jersey (polled)	0.056	0.059	0.074	0.069	0.055	0.176
Jutland	0.058	0.034	0.037	0.106	0.047	0.237
Kampeten: Styrian Bergscheck	0.029	0.036	0.041	0.073	0.038	0.204
Kampeten: Welser Schecken	0.058	0.048	0.045	0.093	0.056	0.227
Kerry	0.045	0.024	0.043	0.092	0.032	0.219
Cretan	0.065	0.051	0.051	0.097	0.049	0.216
Kuhlaender	0.044	0.030	0.036	0.086	0.036	0.214
Landschlag von Warnsdorf	0.060	0.051	0.057	0.085	0.044	0.198
Landschlag von Winkelsdorf	0.068	0.054	0.047	0.109	0.063	0.241
Landschlag X Simmental	0.056	0.047	0.048	0.100	0.055	0.226

Limousin	0.051	0.047	0.056	0.076	0.041	0.190
Moravian Landschlag	0.046	0.041	0.049	0.075	0.040	0.199
Normande	0.051	0.052	0.061	0.077	0.052	0.190
North Wales	0.047	0.026	0.037	0.086	0.025	0.211
White Park	0.058	0.047	0.064	0.095	0.046	0.215
Pinzgauer	0.043	0.035	0.044	0.072	0.032	0.195
Pinzgauer X Scottish Highland	0.055	0.064	0.063	0.078	0.067	0.204
Pinzgauer X Simmentaler	0.056	0.056	0.072	0.068	0.051	0.174
Pinzgauer: Moelltaler	0.052	0.037	0.030	0.088	0.038	0.215
Pinzgauer: Pustertaler	0.061	0.077	0.076	0.064	0.075	0.185
Pirenaica	0.042	0.037	0.045	0.076	0.029	0.199
Red Poll	0.055	0.071	0.071	0.053	0.061	0.179
Maas-Rhein-Ijsselschlag	0.043	0.025	0.040	0.083	0.033	0.208
Danish Red	0.055	0.036	0.044	0.103	0.048	0.230
Angeln	0.040	0.035	0.047	0.074	0.036	0.202
Bohemian Red	0.042	0.030	0.038	0.088	0.036	0.215
Polish Red	0.054	0.036	0.038	0.102	0.044	0.230
Sanga	0.082	0.067	0.060	0.127	0.074	0.258
Sardinian	0.062	0.052	0.053	0.105	0.058	0.231
Scheinfelder	0.058	0.046	0.051	0.097	0.048	0.222
Schoenhengster	0.045	0.032	0.038	0.089	0.041	0.218
Holland Black Pied	0.043	0.044	0.047	0.067	0.042	0.198
Andalusian Black	0.049	0.041	0.039	0.093	0.044	0.227
Sweden (Jaemtland or Vatterbotten)	0.070	0.059	0.072	0.116	0.072	0.234
Scottish Highland	0.053	0.053	0.060	0.055	0.042	0.178
Sicilian	0.065	0.066	0.064	0.080	0.066	0.197
Småland	0.059	0.037	0.053	0.112	0.047	0.235
South Devon	0.058	0.032	0.038	0.098	0.038	0.222
Spanish Fighting Cattle	0.041	0.061	0.065	0.062	0.054	0.192
Buchara Grey	0.125	0.104	0.092	0.163	0.110	0.292
Hungarian Grey	0.050	0.043	0.046	0.075	0.037	0.196
Hungarian Grey X Bern Red Pied	0.071	0.071	0.070	0.078	0.058	0.188
Sudeten	0.050	0.038	0.042	0.089	0.040	0.212
Sudeten X Simmental	0.048	0.052	0.066	0.081	0.052	0.193
Sudeten X Tesstal?	0.058	0.046	0.049	0.083	0.043	0.203
Tarentaise		0.048	0.057	0.070	0.047	0.200
Telemark	0.048		0.037	0.090	0.030	0.217
Tudanca	0.057	0.037		0.091	0.044	0.222
Tuxer	0.070	0.090	0.091		0.082	0.154
Heck	0.047	0.030	0.044	0.082		0.204
Niata	0.200	0.217	0.222	0.154	0.204	
Veredelter Landschlag	0.055	0.047	0.056	0.098	0.049	0.218
Vogtlaender	0.045	0.048	0.060	0.067	0.043	0.183
Waldviertler X Scheinfelder	0.042	0.044	0.052	0.080	0.045	0.207
Watussi	0.058	0.051	0.055	0.102	0.057	0.230
Zebu	0.070	0.053	0.053	0.118	0.060	0.248

Zebu (Africa)	0.069	0.059	0.070	0.115	0.061	0.232
Zebu (Asian)	0.066	0.053	0.060	0.097	0.052	0.209
Zebu (Indian)	0.069	0.054	0.050	0.112	0.061	0.239
Zillertaler	0.047	0.057	0.063	0.050	0.052	0.171

	Veredelter Landschlag	Vogtlaender	Waldviertler X Scheinfelder	Watussi	Zebu	Zebu (Africa)
Ayrshire	0.054	0.037	0.044	0.055	0.068	0.067
Blondvieh: Carinthian	0.042	0.042	0.036	0.039	0.051	0.060
Blondvieh: Lavanttaler	0.045	0.045	0.036	0.044	0.051	0.062
Blondvieh: Mariahofer	0.059	0.040	0.039	0.061	0.072	0.078
Blondvieh: Murbodner	0.041	0.038	0.041	0.041	0.058	0.056
Blondvieh: Waldviertler	0.044	0.048	0.039	0.045	0.045	0.057
Bos primigenius (Aurochs)	0.070	0.079	0.075	0.067	0.074	0.075
Brazilian	0.059	0.051	0.054	0.062	0.073	0.070
Montafon	0.044	0.047	0.041	0.042	0.048	0.057
Buša	0.049	0.056	0.044	0.053	0.041	0.054
Chianina	0.059	0.064	0.061	0.059	0.053	0.069
Chillingham	0.072	0.073	0.063	0.083	0.076	0.085
Devon	0.048	0.035	0.035	0.048	0.057	0.060
Egerlaender	0.057	0.058	0.053	0.047	0.058	0.069
Hérens	0.060	0.040	0.047	0.069	0.078	0.072
Fjällko	0.047	0.051	0.041	0.046	0.045	0.057
Bern Red Pied	0.046	0.044	0.037	0.039	0.052	0.058
Freiburg Red Pied	0.060	0.050	0.055	0.057	0.073	0.075
Simmental	0.050	0.034	0.040	0.056	0.071	0.065
South Moravian Red Pied	0.045	0.041	0.042	0.051	0.062	0.065
Rubia Gallega	0.064	0.081	0.072	0.061	0.054	0.064
Allgaeuer Grey	0.060	0.048	0.044	0.062	0.076	0.081
Krainer Grey	0.061	0.044	0.058	0.063	0.072	0.069
Oberinntaler Grey	0.044	0.036	0.037	0.045	0.061	0.057
Haná-Berne	0.044	0.055	0.051	0.046	0.056	0.057
Iceland	0.049	0.046	0.048	0.061	0.067	0.059
Jersey	0.072	0.043	0.061	0.080	0.091	0.089
Jersey (polled)	0.070	0.045	0.059	0.075	0.087	0.081
Jutland	0.053	0.065	0.053	0.054	0.045	0.063
Kampeten: Styrian Bergscheck	0.046	0.037	0.034	0.047	0.059	0.061
Kampeten: Welser Schecken	0.060	0.067	0.062	0.062	0.066	0.069
Kerry	0.046	0.051	0.043	0.050	0.048	0.051
Cretan	0.061	0.069	0.060	0.073	0.052	0.068
Kuhlaender	0.037	0.040	0.037	0.044	0.051	0.056
Landschlag von Warnsdorf	0.056	0.043	0.047	0.060	0.070	0.072
Landschlag von Winkelsdorf	0.052	0.070	0.057	0.057	0.051	0.070
Landschlag X Simmental	0.048	0.058	0.050	0.050	0.052	0.060
Limousin	0.049	0.029	0.041	0.056	0.072	0.065
Moravian Landschlag	0.043	0.036	0.042	0.053	0.065	0.062
Normande	0.062	0.035	0.046	0.062	0.076	0.079

North Wales	0.041	0.043	0.036	0.050	0.051	0.056
White Park	0.059	0.063	0.050	0.066	0.058	0.068
Pinzgauer	0.046	0.027	0.039	0.051	0.065	0.063
Pinzgauer X Scottish Highland	0.070	0.055	0.059	0.063	0.083	0.085
Pinzgauer X Simmentaler	0.065	0.038	0.055	0.073	0.092	0.081
Pinzgauer: Moelltaler	0.046	0.050	0.044	0.047	0.052	0.060
Pinzgauer: Pustertaler	0.084	0.066	0.070	0.090	0.100	0.098
Pirenaica	0.052	0.035	0.039	0.056	0.063	0.067
Red Poll	0.080	0.061	0.065	0.084	0.096	0.095
Maas-Rhein-Ijsselschlag	0.043	0.038	0.033	0.047	0.052	0.058
Danish Red	0.050	0.056	0.043	0.045	0.044	0.063
Angeln	0.052	0.046	0.045	0.058	0.063	0.061
Bohemian Red	0.038	0.041	0.038	0.041	0.050	0.053
Polish Red	0.039	0.060	0.047	0.049	0.033	0.053
Sanga	0.069	0.091	0.072	0.065	0.039	0.074
Sardinian	0.057	0.062	0.053	0.049	0.052	0.068
Scheinfelder	0.048	0.061	0.047	0.048	0.050	0.050
Schoenhengster	0.041	0.045	0.041	0.041	0.050	0.053
Holland Black Pied	0.057	0.045	0.045	0.061	0.072	0.071
Andalusian Black	0.048	0.059	0.046	0.045	0.048	0.053
Sweden (Jaemtland or Vatterbotten)	0.070	0.072	0.064	0.060	0.067	0.077
Scottish Highland	0.070	0.042	0.058	0.075	0.089	0.082
Sicilian	0.073	0.051	0.067	0.061	0.091	0.088
Småland	0.048	0.067	0.053	0.056	0.043	0.049
South Devon	0.046	0.051	0.045	0.043	0.043	0.057
Spanish Fighting Cattle	0.067	0.053	0.055	0.070	0.084	0.077
Buchara Grey	0.106	0.136	0.116	0.108	0.076	0.107
Hungarian Grey	0.047	0.036	0.041	0.053	0.067	0.061
Hungarian Grey X Bern Red Pied	0.073	0.056	0.069	0.080	0.095	0.085
Sudeten	0.046	0.041	0.045	0.053	0.060	0.068
Sudeten X Simmental	0.058	0.039	0.046	0.065	0.074	0.077
Sudeten X Tesstal?	0.056	0.044	0.052	0.055	0.071	0.072
Tarentaise	0.055	0.045	0.042	0.058	0.070	0.069
Telemark	0.047	0.048	0.044	0.051	0.053	0.059
Tudanca	0.056	0.060	0.052	0.055	0.053	0.070
Tuxer	0.098	0.067	0.080	0.102	0.118	0.115
Heck	0.049	0.043	0.045	0.057	0.060	0.061
Niata	0.218	0.183	0.207	0.230	0.248	0.232
Veredelter Landschlag		0.053	0.048	0.054	0.056	0.051
Vogtlaender	0.053		0.042	0.058	0.079	0.072
Waldviertler X Scheinfelder	0.048	0.042		0.051	0.060	0.065
Watussi	0.054	0.058	0.051		0.054	0.059
Zebu	0.056	0.079	0.060	0.054		0.055
Zebu (Africa)	0.051	0.072	0.065	0.059	0.055	
Zebu (Asian)	0.055	0.056	0.060	0.064	0.062	0.066
Zebu (Indian)	0.059	0.076	0.062	0.057	0.034	0.062

Zillertaler	0.070	0.037	0.056	0.077	0.092	0.087
	Zebu (Asian)	Zebu (Indian)	Zillertaler			
Ayrshire	0.053	0.070	0.051			
Blondvieh: Carinthian	0.055	0.050	0.059			
Blondvieh: Lavanttaler	0.056	0.050	0.058			
Blondvieh: Mariahofer	0.058	0.067	0.043			
Blondvieh: Murbodner	0.052	0.055	0.055			
Blondvieh: Waldviertler	0.055	0.046	0.058			
Bos primigenius (Aurochs)	0.079	0.071	0.080			
Brazilian	0.060	0.065	0.053			
Montafon	0.057	0.045	0.058			
Buša	0.060	0.050	0.064			
Chianina	0.055	0.045	0.068			
Chillingham	0.081	0.080	0.070			
Devon	0.045	0.056	0.051			
Egerlaender	0.066	0.053	0.073			
Hérens	0.068	0.079	0.043			
Fjällko	0.058	0.054	0.067			
Bern Red Pied	0.056	0.049	0.059			
Freiburg Red Pied	0.063	0.063	0.061			
Simmental	0.056	0.066	0.040			
South Moravian Red Pied	0.057	0.056	0.049			
Rubia Gallega	0.074	0.052	0.090			
Allgaeuer Grey	0.069	0.072	0.052			
Krainer Grey	0.061	0.065	0.050			
Oberinntaler Grey	0.057	0.059	0.048			
Haná-Berne	0.062	0.052	0.067			
Iceland	0.061	0.074	0.059			
Jersey	0.065	0.093	0.055			
Jersey (polled)	0.066	0.086	0.049			
Jutland	0.063	0.049	0.075			
Kampeten: Styrian Bergscheck	0.057	0.058	0.045			
Kampeten: Welser Schecken	0.067	0.056	0.067			
Kerry	0.058	0.053	0.062			
Cretan	0.056	0.054	0.072			
Kuhlaender	0.048	0.047	0.054			
Landschlag von Warnsdorf	0.063	0.071	0.062			
Landschlag von Winkelsdorf	0.072	0.053	0.083			
Landschlag X Simmental	0.063	0.049	0.072			
Limousin	0.046	0.069	0.047			
Moravian Landschlag	0.053	0.062	0.051			
Normande	0.052	0.071	0.047			
North Wales	0.049	0.049	0.054			
White Park	0.068	0.069	0.072			
Pinzgauer	0.049	0.060	0.041			
Pinzgauer X Scottish Highland	0.075	0.078	0.060			
Pinzgauer X Simmentaler	0.064	0.087	0.044			

Pinzgauer: Moelltaler	0.051	0.043	0.058			
Pinzgauer: Pustertaler	0.082	0.093	0.049			
Pirenaica	0.050	0.060	0.044			
Red Poll	0.085	0.092	0.054			
Maas-Rhein-Ijsselschlag	0.047	0.054	0.051			
Danish Red	0.059	0.048	0.072			
Angeln	0.062	0.062	0.050			
Bohemian Red	0.054	0.050	0.057			
Polish Red	0.055	0.039	0.072			
Sanga	0.080	0.049	0.102			
Sardinian	0.059	0.050	0.076			
Scheinfelder	0.061	0.051	0.072			
Schoenhengster	0.057	0.048	0.058			
Holland Black Pied	0.063	0.066	0.045			
Andalusian Black	0.063	0.048	0.067			
Sweden (Jaemtland or Vatterbotten)	0.081	0.079	0.090			
Scottish Highland	0.074	0.084	0.036			
Sicilian	0.077	0.086	0.063			
Småland	0.064	0.055	0.080			
South Devon	0.050	0.045	0.067			
Spanish Fighting Cattle	0.078	0.081	0.051			
Buchara Grey	0.112	0.075	0.140			
Hungarian Grey	0.050	0.061	0.049			
Hungarian Grey X Bern Red Pied	0.069	0.086	0.060			
Sudeten	0.057	0.061	0.058			
Sudeten X Simmental	0.063	0.077	0.055			
Sudeten X Tesstal?	0.061	0.065	0.058			
Tarentaise	0.066	0.069	0.047			
Telemark	0.053	0.054	0.057			
Tudanca	0.060	0.050	0.063			
Tuxer	0.097	0.112	0.050			
Heck	0.052	0.061	0.052			
Niata	0.209	0.239	0.171			
Veredelter Landschlag	0.055	0.059	0.070			
Vogtlaender	0.056	0.076	0.037			
Waldviertler X Scheinfelder	0.060	0.062	0.056			
Watussi	0.064	0.057	0.077			
Zebu	0.062	0.034	0.092			
Zebu (Africa)	0.066	0.062	0.087			
Zebu (Asian)		0.058	0.067			
Zebu (Indian)	0.058		0.084			
Zillertaler	0.067	0.084				

Supplementary Table 10: Procrustes distances among lower jaws from cattle breeds represented in morphospace.

	Ayrshire	Blondvieh: Carinthian	Blondvieh: Lavanttaler	Blondvieh: Mariahofer	Blondvieh: Murbodner	Blondvieh: Waldviertler
Ayrshire		0.024	0.036	0.034	0.025	0.022
Blondvieh: Carinthian	0.024		0.025	0.037	0.018	0.029
Blondvieh: Lavanttaler	0.036	0.025		0.043	0.029	0.036
Blondvieh: Mariahofer	0.034	0.037	0.043		0.037	0.030
Blondvieh: Murbodner	0.025	0.018	0.029	0.037		0.030
Blondvieh: Waldviertler	0.022	0.029	0.036	0.030	0.030	
Bos primigenius (Aurochs)	0.068	0.067	0.070	0.088	0.066	0.077
Montafon	0.022	0.032	0.040	0.036	0.035	0.028
Buša	0.030	0.031	0.035	0.038	0.031	0.031
Devon	0.018	0.022	0.032	0.027	0.021	0.023
Egerlaender	0.026	0.023	0.026	0.026	0.024	0.025
Bern Red Pied	0.035	0.029	0.041	0.052	0.026	0.045
Simmental	0.024	0.015	0.027	0.035	0.020	0.031
South Moravian Red Pied	0.021	0.030	0.040	0.033	0.026	0.028
Rubia Gallega	0.033	0.036	0.047	0.053	0.036	0.042
Krainer Grey	0.037	0.028	0.043	0.049	0.031	0.040
Oberinntaler Grey	0.023	0.039	0.047	0.032	0.039	0.025
Guernsey	0.035	0.039	0.045	0.036	0.038	0.036
Iceland	0.027	0.035	0.041	0.035	0.036	0.031
Jersey	0.041	0.050	0.052	0.030	0.049	0.037
Kampeten: Styrian Bergscheck	0.018	0.021	0.030	0.027	0.021	0.018
Kampeten: Welser Schecken	0.030	0.022	0.030	0.049	0.027	0.037
Kerry	0.016	0.025	0.035	0.036	0.026	0.017
Cretan	0.041	0.050	0.061	0.065	0.048	0.053
Kuhlaender	0.030	0.025	0.032	0.030	0.025	0.032
Limousin	0.031	0.031	0.036	0.027	0.030	0.033
Moravian Landschlag	0.029	0.028	0.036	0.038	0.031	0.035
Normande	0.037	0.048	0.055	0.026	0.045	0.036
North Wales	0.025	0.024	0.033	0.035	0.026	0.032
White Park	0.045	0.050	0.053	0.038	0.052	0.047
Pasiega	0.046	0.047	0.055	0.060	0.050	0.052
Pinzgauer	0.036	0.032	0.037	0.035	0.031	0.037
Pinzgauer: Moelltaler	0.032	0.026	0.034	0.029	0.027	0.034
Pirenaica	0.022	0.028	0.035	0.021	0.029	0.022
Maas-Rhein-Ijsselschlag	0.014	0.022	0.035	0.032	0.022	0.027
Danish Red	0.029	0.024	0.034	0.036	0.027	0.031
Angeln	0.036	0.035	0.035	0.032	0.030	0.031
Bohemian Red	0.018	0.019	0.027	0.034	0.022	0.018
Polish Red	0.032	0.036	0.045	0.046	0.034	0.030
Sardinian	0.034	0.030	0.035	0.045	0.035	0.043
Scheinfelder	0.049	0.038	0.044	0.059	0.040	0.055
Schoenhengster	0.032	0.027	0.038	0.031	0.032	0.026

Holland Black Pied	0.032	0.026	0.034	0.031	0.026	0.033
Andalusian Black	0.026	0.026	0.035	0.043	0.027	0.027
Scottish Highland	0.029	0.027	0.037	0.044	0.029	0.038
South Devon	0.024	0.030	0.040	0.043	0.027	0.033
Spanish Fighting Cattle	0.035	0.034	0.045	0.049	0.034	0.041
Buchara Grey	0.039	0.034	0.042	0.055	0.032	0.048
Kalmuek Steppe	0.034	0.042	0.053	0.052	0.035	0.042
Hungarian Grey	0.031	0.031	0.040	0.048	0.023	0.036
Sudeten	0.024	0.028	0.033	0.032	0.031	0.021
Sudeten X Tesstal?	0.044	0.044	0.049	0.040	0.046	0.044
Tarentaise	0.031	0.034	0.039	0.023	0.034	0.031
Telemark	0.015	0.028	0.039	0.034	0.030	0.022
Tesstal	0.031	0.030	0.031	0.030	0.025	0.032
Tudanca	0.034	0.030	0.039	0.054	0.032	0.037
Tuxer	0.084	0.085	0.086	0.075	0.083	0.081
Heck	0.050	0.039	0.043	0.064	0.042	0.055
Niata	0.121	0.131	0.134	0.103	0.126	0.119
Vogtlaender	0.046	0.052	0.055	0.034	0.050	0.045
Walchshofer	0.050	0.049	0.057	0.064	0.051	0.057
Watussi	0.038	0.042	0.061	0.054	0.044	0.050
Zebu	0.028	0.031	0.032	0.039	0.034	0.034
Zebu (India)	0.031	0.037	0.038	0.042	0.034	0.033
Zillertaler	0.048	0.048	0.048	0.039	0.052	0.045
	Bos primigenius (Aurochs)	Montafon	Buša	Devon	Egerlaender	Bern Red Pied
Ayrshire	0.068	0.022	0.030	0.018	0.026	0.035
Blondvieh: Carinthian	0.067	0.032	0.031	0.022	0.023	0.029
Blondvieh: Lavanttaler	0.070	0.040	0.035	0.032	0.026	0.041
Blondvieh: Mariahofer	0.088	0.036	0.038	0.027	0.026	0.052
Blondvieh: Murbodner	0.066	0.035	0.031	0.021	0.024	0.026
Blondvieh: Waldviertler	0.077	0.028	0.031	0.023	0.025	0.045
Bos primigenius (Aurochs)		0.071	0.062	0.074	0.078	0.063
Montafon	0.071		0.033	0.030	0.032	0.047
Buša	0.062	0.033		0.035	0.031	0.044
Devon	0.074	0.030	0.035		0.021	0.033
Egerlaender	0.078	0.032	0.031	0.021		0.041
Bern Red Pied	0.063	0.047	0.044	0.033	0.041	
Simmental	0.067	0.033	0.032	0.020	0.024	0.027
South Moravian Red Pied	0.068	0.030	0.030	0.021	0.029	0.036
Rubia Gallega	0.054	0.032	0.043	0.038	0.046	0.039
Krainer Grey	0.071	0.048	0.043	0.033	0.038	0.038
Oberinntaler Grey	0.080	0.022	0.038	0.027	0.033	0.050
Guernsey	0.079	0.042	0.035	0.032	0.033	0.051
Iceland	0.065	0.028	0.026	0.032	0.036	0.049
Jersey	0.099	0.046	0.050	0.036	0.038	0.066
Kampeten: Styrian Bergscheck	0.073	0.028	0.028	0.017	0.015	0.037

Kampeten: Welser Schecken	0.054	0.038	0.035	0.032	0.036	0.028
Kerry	0.065	0.026	0.027	0.021	0.027	0.037
Cretan	0.056	0.040	0.047	0.052	0.059	0.047
Kuhlaender	0.084	0.039	0.041	0.022	0.021	0.039
Limousin	0.082	0.043	0.042	0.020	0.028	0.040
Moravian Landschlag	0.082	0.042	0.042	0.027	0.029	0.044
Normande	0.091	0.045	0.048	0.030	0.037	0.054
North Wales	0.072	0.039	0.039	0.020	0.029	0.036
White Park	0.083	0.051	0.041	0.045	0.046	0.061
Pasiega	0.065	0.056	0.055	0.044	0.055	0.048
Pinzgauer	0.090	0.049	0.047	0.026	0.029	0.044
Pinzgauer: Moelltaler	0.079	0.039	0.040	0.021	0.026	0.035
Pirenaica	0.076	0.027	0.033	0.017	0.022	0.045
Maas-Rhein-Ijsselschlag	0.067	0.029	0.033	0.015	0.028	0.028
Danish Red	0.063	0.039	0.034	0.024	0.028	0.036
Angeln	0.079	0.040	0.037	0.029	0.034	0.043
Bohemian Red	0.064	0.025	0.025	0.020	0.021	0.036
Polish Red	0.063	0.033	0.031	0.036	0.039	0.046
Sardinian	0.057	0.040	0.038	0.032	0.035	0.037
Scheinfelder	0.051	0.052	0.043	0.047	0.048	0.038
Schoenhengster	0.080	0.040	0.034	0.028	0.028	0.045
Holland Black Pied	0.078	0.043	0.038	0.025	0.030	0.035
Andalusian Black	0.058	0.028	0.031	0.028	0.033	0.037
Scottish Highland	0.058	0.038	0.039	0.028	0.039	0.031
South Devon	0.062	0.036	0.042	0.023	0.036	0.030
Spanish Fighting Cattle	0.046	0.039	0.031	0.039	0.042	0.040
Buchara Grey	0.057	0.046	0.045	0.039	0.047	0.036
Kalmuek Steppe	0.068	0.040	0.037	0.040	0.046	0.041
Hungarian Grey	0.067	0.037	0.040	0.030	0.038	0.029
Sudeten	0.083	0.034	0.038	0.023	0.022	0.046
Sudeten X Tesstal?	0.095	0.051	0.056	0.038	0.043	0.059
Tarentaise	0.090	0.040	0.039	0.026	0.021	0.047
Telemark	0.069	0.027	0.031	0.021	0.030	0.041
Tesstal	0.080	0.042	0.035	0.024	0.026	0.042
Tudanca	0.056	0.043	0.034	0.038	0.042	0.030
Tuxer	0.141	0.096	0.092	0.078	0.074	0.093
Heck	0.056	0.058	0.047	0.049	0.054	0.034
Niata	0.179	0.123	0.130	0.115	0.116	0.134
Vogtlaender	0.106	0.056	0.058	0.038	0.039	0.062
Walchshofer	0.056	0.049	0.057	0.050	0.061	0.052
Watussi	0.077	0.049	0.051	0.043	0.050	0.044
Zebu	0.066	0.033	0.028	0.032	0.035	0.041
Zebu (India)	0.065	0.032	0.030	0.032	0.037	0.041
Zillertaler	0.100	0.057	0.055	0.041	0.041	0.061

	Simmental	South Moravian Red Pied	Rubia Gallega	Krainer Grey	Oberinntaler Grey	Guernsey
Ayrshire	0.024	0.021	0.033	0.037	0.023	0.035

Blondvieh: Carinthian	0.015	0.030	0.036	0.028	0.039	0.039
Blondvieh: Lavanttaler	0.027	0.040	0.047	0.043	0.047	0.045
Blondvieh: Mariahofer	0.035	0.033	0.053	0.049	0.032	0.036
Blondvieh: Murbodner	0.020	0.026	0.036	0.031	0.039	0.038
Blondvieh: Waldviertler	0.031	0.028	0.042	0.040	0.025	0.036
Bos primigenius (Aurochs)	0.067	0.068	0.054	0.071	0.080	0.079
Montafon	0.033	0.030	0.032	0.048	0.022	0.042
Buša	0.032	0.030	0.043	0.043	0.038	0.035
Devon	0.020	0.021	0.038	0.033	0.027	0.032
Egerlaender	0.024	0.029	0.046	0.038	0.033	0.033
Bern Red Pied	0.027	0.036	0.039	0.038	0.050	0.051
Simmental		0.028	0.038	0.030	0.037	0.037
South Moravian Red Pied	0.028		0.036	0.038	0.027	0.030
Rubia Gallega	0.038	0.036		0.045	0.041	0.052
Krainer Grey	0.030	0.038	0.045		0.048	0.039
Oberinntaler Grey	0.037	0.027	0.041	0.048		0.036
Guernsey	0.037	0.030	0.052	0.039	0.036	
Iceland	0.036	0.028	0.037	0.045	0.032	0.037
Jersey	0.048	0.042	0.063	0.053	0.035	0.033
Kampeten: Styrian Bergscheck	0.023	0.025	0.040	0.035	0.027	0.033
Kampeten: Welser Schecken	0.025	0.036	0.032	0.038	0.046	0.050
Kerry	0.026	0.023	0.033	0.034	0.026	0.034
Cretan	0.050	0.046	0.030	0.058	0.047	0.061
Kuhlaender	0.024	0.035	0.048	0.036	0.037	0.037
Limousin	0.026	0.031	0.050	0.038	0.039	0.037
Moravian Landschlag	0.029	0.036	0.049	0.034	0.039	0.036
Normande	0.043	0.033	0.057	0.053	0.032	0.037
North Wales	0.027	0.030	0.042	0.033	0.039	0.040
White Park	0.048	0.046	0.065	0.061	0.050	0.048
Pasiega	0.044	0.045	0.049	0.046	0.055	0.048
Pinzgauer	0.031	0.039	0.057	0.034	0.045	0.038
Pinzgauer: Moelltaler	0.021	0.031	0.045	0.038	0.037	0.039
Pirenaica	0.028	0.025	0.040	0.037	0.025	0.029
Maas-Rhein-Ijsselschlag	0.019	0.021	0.032	0.034	0.030	0.035
Danish Red	0.025	0.030	0.040	0.033	0.042	0.039
Angeln	0.032	0.035	0.045	0.042	0.041	0.043
Bohemian Red	0.022	0.024	0.032	0.034	0.030	0.037
Polish Red	0.039	0.028	0.035	0.039	0.036	0.041
Sardinian	0.027	0.032	0.040	0.044	0.045	0.040
Scheinfelder	0.034	0.046	0.047	0.042	0.059	0.052
Schoenhengster	0.028	0.035	0.051	0.033	0.039	0.036
Holland Black Pied	0.028	0.033	0.049	0.038	0.044	0.043
Andalusian Black	0.030	0.025	0.027	0.039	0.033	0.042
Scottish Highland	0.025	0.029	0.033	0.038	0.042	0.044
South Devon	0.030	0.029	0.031	0.037	0.038	0.045
Spanish Fighting Cattle	0.035	0.033	0.034	0.040	0.045	0.043

Buchara Grey	0.035	0.041	0.036	0.032	0.053	0.049
Kalmuek Steppe	0.040	0.032	0.037	0.041	0.039	0.043
Hungarian Grey	0.029	0.030	0.030	0.034	0.038	0.044
Sudeten	0.032	0.034	0.048	0.037	0.033	0.036
Sudeten X Tesstal?	0.047	0.046	0.055	0.049	0.048	0.050
Tarentaise	0.031	0.034	0.057	0.046	0.034	0.032
Telemark	0.030	0.022	0.035	0.035	0.025	0.033
Tesstal	0.028	0.032	0.048	0.037	0.041	0.035
Tudanca	0.032	0.036	0.038	0.040	0.048	0.049
Tuxer	0.082	0.088	0.110	0.083	0.086	0.078
Heck	0.037	0.050	0.049	0.045	0.064	0.059
Niata	0.124	0.118	0.140	0.135	0.110	0.115
Vogtlaender	0.048	0.049	0.072	0.055	0.046	0.043
Walchshofer	0.049	0.047	0.029	0.053	0.056	0.062
Watussi	0.040	0.042	0.052	0.042	0.047	0.045
Zebu	0.029	0.036	0.045	0.049	0.039	0.044
Zebu (India)	0.033	0.028	0.038	0.050	0.035	0.045
Zillertaler	0.045	0.052	0.073	0.054	0.052	0.047

	Iceland	Jersey	Kampeten: Styrian Bergscheck	Kampeten: Welser Schecken	Kerry	Cretan
Ayrshire	0.027	0.041	0.018	0.030	0.016	0.041
Blondvieh: Carinthian	0.035	0.050	0.021	0.022	0.025	0.050
Blondvieh: Lavanttaler	0.041	0.052	0.030	0.030	0.035	0.061
Blondvieh: Mariahofer	0.035	0.030	0.027	0.049	0.036	0.065
Blondvieh: Murbodner	0.036	0.049	0.021	0.027	0.026	0.048
Blondvieh: Waldviertler	0.031	0.037	0.018	0.037	0.017	0.053
Bos primigenius (Aurochs)	0.065	0.099	0.073	0.054	0.065	0.056
Montafon	0.028	0.046	0.028	0.038	0.026	0.040
Buša	0.026	0.050	0.028	0.035	0.027	0.047
Devon	0.032	0.036	0.017	0.032	0.021	0.052
Egerlaender	0.036	0.038	0.015	0.036	0.027	0.059
Bern Red Pied	0.049	0.066	0.037	0.028	0.037	0.047
Simmental	0.036	0.048	0.023	0.025	0.026	0.050
South Moravian Red Pied	0.028	0.042	0.025	0.036	0.023	0.046
Rubia Gallega	0.037	0.063	0.040	0.032	0.033	0.030
Krainer Grey	0.045	0.053	0.035	0.038	0.034	0.058
Oberinntaler Grey	0.032	0.035	0.027	0.046	0.026	0.047
Guernsey	0.037	0.033	0.033	0.050	0.034	0.061
Iceland		0.042	0.032	0.038	0.029	0.045
Jersey	0.042		0.039	0.063	0.043	0.073
Kampeten: Styrian Bergscheck	0.032	0.039		0.031	0.017	0.051
Kampeten: Welser Schecken	0.038	0.063	0.031		0.029	0.045
Kerry	0.029	0.043	0.017	0.029		0.044
Cretan	0.045	0.073	0.051	0.045	0.044	
Kuhlaender	0.043	0.037	0.024	0.041	0.034	0.059
Limousin	0.037	0.035	0.029	0.041	0.035	0.063

Moravian Landschlag	0.039	0.036	0.029	0.041	0.035	0.059
Normande	0.041	0.031	0.035	0.055	0.039	0.066
North Wales	0.033	0.042	0.027	0.032	0.029	0.056
White Park	0.036	0.048	0.046	0.054	0.048	0.069
Pasiega	0.049	0.064	0.049	0.045	0.046	0.059
Pinzgauer	0.047	0.036	0.031	0.046	0.039	0.070
Pinzgauer: Moelltaler	0.040	0.042	0.027	0.039	0.035	0.056
Pirenaica	0.024	0.028	0.020	0.039	0.024	0.054
Maas-Rhein-Ijsselschlag	0.029	0.043	0.021	0.027	0.021	0.044
Danish Red	0.034	0.050	0.024	0.026	0.025	0.057
Angeln	0.036	0.041	0.033	0.043	0.034	0.057
Bohemian Red	0.027	0.045	0.015	0.023	0.013	0.046
Polish Red	0.035	0.054	0.032	0.039	0.022	0.044
Sardinian	0.039	0.057	0.034	0.031	0.034	0.054
Scheinfelder	0.049	0.073	0.048	0.036	0.047	0.056
Schoenhengster	0.040	0.042	0.024	0.040	0.028	0.062
Holland Black Pied	0.038	0.045	0.028	0.037	0.034	0.060
Andalusian Black	0.033	0.054	0.026	0.026	0.020	0.042
Scottish Highland	0.032	0.055	0.034	0.026	0.032	0.044
South Devon	0.038	0.054	0.028	0.027	0.024	0.048
Spanish Fighting Cattle	0.036	0.062	0.036	0.033	0.030	0.041
Buchara Grey	0.043	0.063	0.043	0.035	0.040	0.051
Kalmuek Steppe	0.040	0.056	0.041	0.046	0.035	0.036
Hungarian Grey	0.041	0.055	0.034	0.034	0.031	0.040
Sudeten	0.038	0.033	0.020	0.040	0.025	0.061
Sudeten X Tesstal?	0.045	0.037	0.044	0.056	0.049	0.071
Tarentaise	0.043	0.031	0.024	0.047	0.035	0.065
Telemark	0.024	0.039	0.022	0.033	0.016	0.045
Tesstal	0.036	0.037	0.026	0.041	0.033	0.061
Tudanca	0.041	0.065	0.036	0.022	0.029	0.043
Tuxer	0.096	0.065	0.077	0.099	0.086	0.117
Heck	0.051	0.074	0.052	0.035	0.049	0.054
Niata	0.126	0.097	0.119	0.142	0.126	0.144
Vogtlaender	0.057	0.028	0.041	0.065	0.050	0.081
Walchshofer	0.046	0.072	0.057	0.046	0.049	0.047
Watussi	0.051	0.058	0.044	0.051	0.043	0.050
Zebu	0.031	0.051	0.030	0.031	0.031	0.048
Zebu (India)	0.034	0.054	0.034	0.033	0.027	0.044
Zillertaler	0.052	0.038	0.044	0.059	0.051	0.081

	Kuhlaender	Limousin	Moravian Landschlag	Normande	North Wales	White Park
Ayrshire	0.030	0.031	0.029	0.037	0.025	0.045
Blondvieh: Carinthian	0.025	0.031	0.028	0.048	0.024	0.050
Blondvieh: Lavanttaler	0.032	0.036	0.036	0.055	0.033	0.053
Blondvieh: Mariahofer	0.030	0.027	0.038	0.026	0.035	0.038
Blondvieh: Murbodner	0.025	0.030	0.031	0.045	0.026	0.052
Blondvieh: Waldviertler	0.032	0.033	0.035	0.036	0.032	0.047

Bos primigenius (Aurochs)	0.084	0.082	0.082	0.091	0.072	0.083
Montafon	0.039	0.043	0.042	0.045	0.039	0.051
Buša	0.041	0.042	0.042	0.048	0.039	0.041
Devon	0.022	0.020	0.027	0.030	0.020	0.045
Egerlaender	0.021	0.028	0.029	0.037	0.029	0.046
Bern Red Pied	0.039	0.040	0.044	0.054	0.036	0.061
Simmental	0.024	0.026	0.029	0.043	0.027	0.048
South Moravian Red Pied	0.035	0.031	0.036	0.033	0.030	0.046
Rubia Gallega	0.048	0.050	0.049	0.057	0.042	0.065
Krainer Grey	0.036	0.038	0.034	0.053	0.033	0.061
Oberinntaler Grey	0.037	0.039	0.039	0.032	0.039	0.050
Guernsey	0.037	0.037	0.036	0.037	0.040	0.048
Iceland	0.043	0.037	0.039	0.041	0.033	0.036
Jersey	0.037	0.035	0.036	0.031	0.042	0.048
Kampeten: Styrian Bergscheck	0.024	0.029	0.029	0.035	0.027	0.046
Kampeten: Welser Schecken	0.041	0.041	0.041	0.055	0.032	0.054
Kerry	0.034	0.035	0.035	0.039	0.029	0.048
Cretan	0.059	0.063	0.059	0.066	0.056	0.069
Kuhlaender		0.025	0.022	0.039	0.028	0.052
Limousin	0.025		0.027	0.030	0.026	0.040
Moravian Landschlag	0.022	0.027		0.043	0.026	0.051
Normande	0.039	0.030	0.043		0.041	0.041
North Wales	0.028	0.026	0.026	0.041		0.045
White Park	0.052	0.040	0.051	0.041	0.045	
Pasiega	0.055	0.050	0.052	0.057	0.046	0.061
Pinzgauer	0.021	0.024	0.022	0.042	0.025	0.053
Pinzgauer: Moelltaler	0.018	0.024	0.028	0.038	0.030	0.051
Pirenaica	0.025	0.025	0.028	0.030	0.023	0.042
Maas-Rhein-Ijsselschlag	0.030	0.024	0.030	0.034	0.023	0.043
Danish Red	0.036	0.031	0.039	0.041	0.025	0.043
Angeln	0.032	0.029	0.038	0.042	0.033	0.047
Bohemian Red	0.030	0.033	0.033	0.042	0.026	0.046
Polish Red	0.048	0.049	0.049	0.051	0.042	0.059
Sardinian	0.041	0.040	0.043	0.049	0.037	0.052
Scheinfelder	0.051	0.050	0.054	0.064	0.049	0.060
Schoenhengster	0.032	0.034	0.036	0.043	0.031	0.046
Holland Black Pied	0.027	0.024	0.032	0.040	0.020	0.041
Andalusian Black	0.040	0.043	0.043	0.049	0.034	0.056
Scottish Highland	0.039	0.033	0.038	0.047	0.029	0.048
South Devon	0.040	0.035	0.042	0.042	0.028	0.054
Spanish Fighting Cattle	0.048	0.049	0.048	0.055	0.041	0.054
Buchara Grey	0.046	0.045	0.045	0.061	0.034	0.062
Kalmuek Steppe	0.045	0.048	0.045	0.052	0.043	0.061
Hungarian Grey	0.035	0.040	0.039	0.051	0.036	0.063
Sudeten	0.027	0.032	0.028	0.041	0.026	0.050
Sudeten X Tesstal?	0.038	0.034	0.032	0.046	0.035	0.057

Tarentaise	0.022	0.027	0.029	0.030	0.035	0.044
Telemark	0.035	0.033	0.033	0.036	0.023	0.043
Tesstal	0.025	0.022	0.026	0.040	0.025	0.047
Tudanca	0.047	0.047	0.048	0.057	0.040	0.056
Tuxer	0.067	0.072	0.069	0.076	0.079	0.090
Heck	0.052	0.051	0.052	0.069	0.045	0.060
Niata	0.113	0.110	0.119	0.094	0.124	0.117
Vogtlaender	0.034	0.035	0.038	0.033	0.044	0.053
Walchshofer	0.061	0.058	0.059	0.066	0.052	0.072
Watussi	0.044	0.049	0.043	0.053	0.044	0.059
Zebu	0.039	0.037	0.039	0.046	0.035	0.037
Zebu (India)	0.044	0.042	0.049	0.045	0.041	0.048
Zillertaler	0.040	0.032	0.040	0.042	0.043	0.040

	Pasiega	Pinzgauer	Pinzgauer: Moelltaler	Pirenaica	Maas-Rhein-Ijsselschlag	Danish Red
Ayrshire	0.046	0.036	0.032	0.022	0.014	0.029
Blondvieh: Carinthian	0.047	0.032	0.026	0.028	0.022	0.024
Blondvieh: Lavanttaler	0.055	0.037	0.034	0.035	0.035	0.034
Blondvieh: Mariahofer	0.060	0.035	0.029	0.021	0.032	0.036
Blondvieh: Murbodner	0.050	0.031	0.027	0.029	0.022	0.027
Blondvieh: Waldviertler	0.052	0.037	0.034	0.022	0.027	0.031
Bos primigenius (Aurochs)	0.065	0.090	0.079	0.076	0.067	0.063
Montafon	0.056	0.049	0.039	0.027	0.029	0.039
Buša	0.055	0.047	0.040	0.033	0.033	0.034
Devon	0.044	0.026	0.021	0.017	0.015	0.024
Egerlaender	0.055	0.029	0.026	0.022	0.028	0.028
Bern Red Pied	0.048	0.044	0.035	0.045	0.028	0.036
Simmental	0.044	0.031	0.021	0.028	0.019	0.025
South Moravian Red Pied	0.045	0.039	0.031	0.025	0.021	0.030
Rubia Gallega	0.049	0.057	0.045	0.040	0.032	0.040
Krainer Grey	0.046	0.034	0.038	0.037	0.034	0.033
Oberinntaler Grey	0.055	0.045	0.037	0.025	0.030	0.042
Guernsey	0.048	0.038	0.039	0.029	0.035	0.039
Iceland	0.049	0.047	0.040	0.024	0.029	0.034
Jersey	0.064	0.036	0.042	0.028	0.043	0.050
Kampeten: Styrian Bergscheck	0.049	0.031	0.027	0.020	0.021	0.024
Kampeten: Welser Schecken	0.045	0.046	0.039	0.039	0.027	0.026
Kerry	0.046	0.039	0.035	0.024	0.021	0.025
Cretan	0.059	0.070	0.056	0.054	0.044	0.057
Kuhlaender	0.055	0.021	0.018	0.025	0.030	0.036
Limousin	0.050	0.024	0.024	0.025	0.024	0.031
Moravian Landschlag	0.052	0.022	0.028	0.028	0.030	0.039
Normande	0.057	0.042	0.038	0.030	0.034	0.041
North Wales	0.046	0.025	0.030	0.023	0.023	0.025
White Park	0.061	0.053	0.051	0.042	0.043	0.043
Pasiega		0.055	0.049	0.047	0.042	0.042

Pinzgauer	0.055		0.027	0.030	0.034	0.038
Pinzgauer: Moelltaler	0.049	0.027		0.027	0.027	0.035
Pirenaica	0.047	0.030	0.027		0.024	0.028
Maas-Rhein-Ijsselschlag	0.042	0.034	0.027	0.024		0.025
Danish Red	0.042	0.038	0.035	0.028	0.025	
Angeln	0.060	0.036	0.032	0.029	0.032	0.038
Bohemian Red	0.047	0.038	0.032	0.022	0.022	0.021
Polish Red	0.053	0.051	0.046	0.036	0.036	0.036
Sardinian	0.037	0.048	0.036	0.036	0.030	0.028
Scheinfelder	0.045	0.057	0.046	0.051	0.044	0.040
Schoenhengster	0.053	0.030	0.035	0.028	0.031	0.029
Holland Black Pied	0.055	0.027	0.029	0.029	0.027	0.030
Andalusian Black	0.045	0.048	0.037	0.031	0.028	0.029
Scottish Highland	0.034	0.043	0.033	0.033	0.023	0.030
South Devon	0.046	0.043	0.038	0.032	0.020	0.023
Spanish Fighting Cattle	0.049	0.056	0.046	0.040	0.035	0.032
Buchara Grey	0.047	0.046	0.045	0.042	0.035	0.038
Kalmuek Steppe	0.059	0.050	0.045	0.042	0.035	0.049
Hungarian Grey	0.051	0.042	0.032	0.037	0.030	0.040
Sudeten	0.056	0.026	0.035	0.023	0.029	0.033
Sudeten X Tesstal?	0.067	0.035	0.041	0.034	0.042	0.050
Tarentaise	0.058	0.027	0.028	0.028	0.031	0.038
Telemark	0.044	0.037	0.037	0.020	0.020	0.027
Tesstal	0.056	0.022	0.027	0.026	0.027	0.034
Tudanca	0.045	0.051	0.044	0.045	0.033	0.033
Tuxer	0.103	0.058	0.076	0.079	0.085	0.088
Heck	0.049	0.056	0.048	0.055	0.044	0.046
Niata	0.139	0.112	0.113	0.115	0.120	0.130
Vogtlaender	0.068	0.030	0.042	0.038	0.046	0.052
Walchshofer	0.050	0.067	0.054	0.051	0.047	0.051
Watussi	0.049	0.048	0.046	0.046	0.039	0.049
Zebu	0.050	0.045	0.038	0.035	0.028	0.034
Zebu (India)	0.054	0.051	0.040	0.037	0.031	0.036
Zillertaler	0.060	0.036	0.042	0.040	0.046	0.048
	Angeln	Bohemian Red	Polish Red	Sardinian	Scheinfelder	Schoenhengster
Ayrshire	0.036	0.018	0.032	0.034	0.049	0.032
Blondvieh: Carinthian	0.035	0.019	0.036	0.030	0.038	0.027
Blondvieh: Lavanttaler	0.035	0.027	0.045	0.035	0.044	0.038
Blondvieh: Mariahofer	0.032	0.034	0.046	0.045	0.059	0.031
Blondvieh: Murbodner	0.030	0.022	0.034	0.035	0.040	0.032
Blondvieh: Waldviertler	0.031	0.018	0.030	0.043	0.055	0.026
Bos primigenius (Aurochs)	0.079	0.064	0.063	0.057	0.051	0.080
Montafon	0.040	0.025	0.033	0.040	0.052	0.040
Buša	0.037	0.025	0.031	0.038	0.043	0.034
Devon	0.029	0.020	0.036	0.032	0.047	0.028
Egerlaender	0.034	0.021	0.039	0.035	0.048	0.028

Bern Red Pied	0.043	0.036	0.046	0.037	0.038	0.045
Simmental	0.032	0.022	0.039	0.027	0.034	0.028
South Moravian Red Pied	0.035	0.024	0.028	0.032	0.046	0.035
Rubia Gallega	0.045	0.032	0.035	0.040	0.047	0.051
Krainer Grey	0.042	0.034	0.039	0.044	0.042	0.033
Oberinntaler Grey	0.041	0.030	0.036	0.045	0.059	0.039
Guernsey	0.043	0.037	0.041	0.040	0.052	0.036
Iceland	0.036	0.027	0.035	0.039	0.049	0.040
Jersey	0.041	0.045	0.054	0.057	0.073	0.042
Kampeten: Styrian Bergscheck	0.033	0.015	0.032	0.034	0.048	0.024
Kampeten: Welser Schecken	0.043	0.023	0.039	0.031	0.036	0.040
Kerry	0.034	0.013	0.022	0.034	0.047	0.028
Cretan	0.057	0.046	0.044	0.054	0.056	0.062
Kuhlaender	0.032	0.030	0.048	0.041	0.051	0.032
Limousin	0.029	0.033	0.049	0.040	0.050	0.034
Moravian Landschlag	0.038	0.033	0.049	0.043	0.054	0.036
Normande	0.042	0.042	0.051	0.049	0.064	0.043
North Wales	0.033	0.026	0.042	0.037	0.049	0.031
White Park	0.047	0.046	0.059	0.052	0.060	0.046
Pasiega	0.060	0.047	0.053	0.037	0.045	0.053
Pinzgauer	0.036	0.038	0.051	0.048	0.057	0.030
Pinzgauer: Moelltaler	0.032	0.032	0.046	0.036	0.046	0.035
Pirenaica	0.029	0.022	0.036	0.036	0.051	0.028
Maas-Rhein-Ijsselschlag	0.032	0.022	0.036	0.030	0.044	0.031
Danish Red	0.038	0.021	0.036	0.028	0.040	0.029
Angeln		0.032	0.042	0.050	0.053	0.035
Bohemian Red	0.032		0.027	0.031	0.044	0.027
Polish Red	0.042	0.027		0.044	0.050	0.037
Sardinian	0.050	0.031	0.044		0.035	0.043
Scheinfelder	0.053	0.044	0.050	0.035		0.051
Schoenhengster	0.035	0.027	0.037	0.043	0.051	
Holland Black Pied	0.026	0.030	0.046	0.043	0.050	0.028
Andalusian Black	0.040	0.018	0.024	0.030	0.042	0.038
Scottish Highland	0.039	0.030	0.041	0.027	0.034	0.042
South Devon	0.040	0.025	0.035	0.034	0.047	0.039
Spanish Fighting Cattle	0.046	0.030	0.031	0.034	0.037	0.043
Buchara Grey	0.042	0.038	0.042	0.042	0.038	0.044
Kalmuek Steppe	0.041	0.039	0.033	0.052	0.053	0.046
Hungarian Grey	0.034	0.031	0.035	0.044	0.045	0.044
Sudeten	0.035	0.024	0.039	0.044	0.059	0.024
Sudeten X Tesstal?	0.039	0.046	0.060	0.058	0.070	0.047
Tarentaise	0.038	0.034	0.050	0.044	0.058	0.030
Telemark	0.034	0.019	0.027	0.038	0.050	0.029
Tesstal	0.025	0.032	0.043	0.044	0.052	0.031
Tudanca	0.046	0.029	0.036	0.038	0.040	0.041
Tuxer	0.081	0.088	0.099	0.098	0.108	0.073

Heck	0.049	0.045	0.056	0.044	0.033	0.052
Niata	0.119	0.129	0.135	0.133	0.148	0.122
Vogtlaender	0.048	0.051	0.064	0.060	0.074	0.041
Walchshofer	0.056	0.048	0.049	0.045	0.048	0.064
Watussi	0.057	0.046	0.052	0.049	0.056	0.045
Zebu	0.039	0.029	0.044	0.036	0.044	0.039
Zebu (India)	0.038	0.028	0.033	0.040	0.049	0.042
Zillertaler	0.047	0.049	0.066	0.055	0.065	0.042
	Holland	Andalusian	Scottish	South Devon	Spanish Fighting	Buchara Grey
	Black Pied	Black	Highland		Cattle	
Ayrshire	0.032	0.026	0.029	0.024	0.035	0.039
Blondvieh: Carinthian	0.026	0.026	0.027	0.030	0.034	0.034
Blondvieh: Lavanttaler	0.034	0.035	0.037	0.040	0.045	0.042
Blondvieh: Mariahofer	0.031	0.043	0.044	0.043	0.049	0.055
Blondvieh: Murbodner	0.026	0.027	0.029	0.027	0.034	0.032
Blondvieh: Waldviertler	0.033	0.027	0.038	0.033	0.041	0.048
Bos primigenius (Aurochs)	0.078	0.058	0.058	0.062	0.046	0.057
Montafon	0.043	0.028	0.038	0.036	0.039	0.046
Buša	0.038	0.031	0.039	0.042	0.031	0.045
Devon	0.025	0.028	0.028	0.023	0.039	0.039
Egerlaender	0.030	0.033	0.039	0.036	0.042	0.047
Bern Red Pied	0.035	0.037	0.031	0.030	0.040	0.036
Simmental	0.028	0.030	0.025	0.030	0.035	0.035
South Moravian Red Pied	0.033	0.025	0.029	0.029	0.033	0.041
Rubia Gallega	0.049	0.027	0.033	0.031	0.034	0.036
Krainer Grey	0.038	0.039	0.038	0.037	0.040	0.032
Oberinntaler Grey	0.044	0.033	0.042	0.038	0.045	0.053
Guernsey	0.043	0.042	0.044	0.045	0.043	0.049
Iceland	0.038	0.033	0.032	0.038	0.036	0.043
Jersey	0.045	0.054	0.055	0.054	0.062	0.063
Kampeten: Styrian Bergscheck	0.028	0.026	0.034	0.028	0.036	0.043
Kampeten: Welser Schecken	0.037	0.026	0.026	0.027	0.033	0.035
Kerry	0.034	0.020	0.032	0.024	0.030	0.040
Cretan	0.060	0.042	0.044	0.048	0.041	0.051
Kuhlaender	0.027	0.040	0.039	0.040	0.048	0.046
Limousin	0.024	0.043	0.033	0.035	0.049	0.045
Moravian Landschlag	0.032	0.043	0.038	0.042	0.048	0.045
Normande	0.040	0.049	0.047	0.042	0.055	0.061
North Wales	0.020	0.034	0.029	0.028	0.041	0.034
White Park	0.041	0.056	0.048	0.054	0.054	0.062
Pasiega	0.055	0.045	0.034	0.046	0.049	0.047
Pinzgauer	0.027	0.048	0.043	0.043	0.056	0.046
Pinzgauer: Moelltaler	0.029	0.037	0.033	0.038	0.046	0.045
Pirenaica	0.029	0.031	0.033	0.032	0.040	0.042
Maas-Rhein-Ijsselschlag	0.027	0.028	0.023	0.020	0.035	0.035
Danish Red	0.030	0.029	0.030	0.023	0.032	0.038

Angeln	0.026	0.040	0.039	0.040	0.046	0.042
Bohemian Red	0.030	0.018	0.030	0.025	0.030	0.038
Polish Red	0.046	0.024	0.041	0.035	0.031	0.042
Sardinian	0.043	0.030	0.027	0.034	0.034	0.042
Scheinfelder	0.050	0.042	0.034	0.047	0.037	0.038
Schoenhengster	0.028	0.038	0.042	0.039	0.043	0.044
Holland Black Pied		0.039	0.034	0.036	0.044	0.040
Andalusian Black	0.039		0.029	0.027	0.026	0.039
Scottish Highland	0.034	0.029		0.030	0.034	0.034
South Devon	0.036	0.027	0.030		0.035	0.035
Spanish Fighting Cattle	0.044	0.026	0.034	0.035		0.039
Buchara Grey	0.040	0.039	0.034	0.035	0.039	
Kalmuek Steppe	0.045	0.039	0.044	0.043	0.040	0.039
Hungarian Grey	0.039	0.030	0.033	0.033	0.039	0.035
Sudeten	0.030	0.036	0.043	0.036	0.048	0.046
Sudeten X Tesstal?	0.039	0.054	0.049	0.051	0.062	0.053
Tarentaise	0.031	0.044	0.046	0.044	0.052	0.056
Telemark	0.031	0.027	0.031	0.026	0.034	0.037
Tesstal	0.024	0.041	0.038	0.037	0.047	0.040
Tudanca	0.042	0.030	0.033	0.035	0.036	0.042
Tuxer	0.075	0.099	0.097	0.094	0.105	0.100
Heck	0.045	0.047	0.033	0.051	0.044	0.040
Niata	0.120	0.135	0.132	0.130	0.144	0.144
Vogtlaender	0.042	0.062	0.060	0.056	0.068	0.066
Walchshofer	0.061	0.041	0.037	0.045	0.045	0.043
Watussi	0.047	0.049	0.043	0.050	0.047	0.051
Zebu	0.035	0.036	0.033	0.038	0.040	0.046
Zebu (India)	0.042	0.030	0.037	0.034	0.040	0.048
Zillertaler	0.040	0.061	0.052	0.058	0.068	0.065

	Kalmuek Steppe	Hungarian Grey	Sudeten	Sudeten X Tesstal?	Tarentaise	Telemark
Ayrshire	0.034	0.031	0.024	0.044	0.031	0.015
Blondvieh: Carinthian	0.042	0.031	0.028	0.044	0.034	0.028
Blondvieh: Lavanttaler	0.053	0.040	0.033	0.049	0.039	0.039
Blondvieh: Mariahofer	0.052	0.048	0.032	0.040	0.023	0.034
Blondvieh: Murbodner	0.035	0.023	0.031	0.046	0.034	0.030
Blondvieh: Waldviertler	0.042	0.036	0.021	0.044	0.031	0.022
Bos primigenius (Aurochs)	0.068	0.067	0.083	0.095	0.090	0.069
Montafon	0.040	0.037	0.034	0.051	0.040	0.027
Buša	0.037	0.040	0.038	0.056	0.039	0.031
Devon	0.040	0.030	0.023	0.038	0.026	0.021
Egerlaender	0.046	0.038	0.022	0.043	0.021	0.030
Bern Red Pied	0.041	0.029	0.046	0.059	0.047	0.041
Simmental	0.040	0.029	0.032	0.047	0.031	0.030
South Moravian Red Pied	0.032	0.030	0.034	0.046	0.034	0.022
Rubia Gallega	0.037	0.030	0.048	0.055	0.057	0.035

Krainer Grey	0.041	0.034	0.037	0.049	0.046	0.035
Oberinntaler Grey	0.039	0.038	0.033	0.048	0.034	0.025
Guernsey	0.043	0.044	0.036	0.050	0.032	0.033
Iceland	0.040	0.041	0.038	0.045	0.043	0.024
Jersey	0.056	0.055	0.033	0.037	0.031	0.039
Kampeten: Styrian Bergscheck	0.041	0.034	0.020	0.044	0.024	0.022
Kampeten: Welser Schecken	0.046	0.034	0.040	0.056	0.047	0.033
Kerry	0.035	0.031	0.025	0.049	0.035	0.016
Cretan	0.036	0.040	0.061	0.071	0.065	0.045
Kuhlaender	0.045	0.035	0.027	0.038	0.022	0.035
Limousin	0.048	0.040	0.032	0.034	0.027	0.033
Moravian Landschlag	0.045	0.039	0.028	0.032	0.029	0.033
Normande	0.052	0.051	0.041	0.046	0.030	0.036
North Wales	0.043	0.036	0.026	0.035	0.035	0.023
White Park	0.061	0.063	0.050	0.057	0.044	0.043
Pasiega	0.059	0.051	0.056	0.067	0.058	0.044
Pinzgauer	0.050	0.042	0.026	0.035	0.027	0.037
Pinzgauer: Moelltaler	0.045	0.032	0.035	0.041	0.028	0.037
Pirenaica	0.042	0.037	0.023	0.034	0.028	0.020
Maas-Rhein-Ijsselschlag	0.035	0.030	0.029	0.042	0.031	0.020
Danish Red	0.049	0.040	0.033	0.050	0.038	0.027
Angeln	0.041	0.034	0.035	0.039	0.038	0.034
Bohemian Red	0.039	0.031	0.024	0.046	0.034	0.019
Polish Red	0.033	0.035	0.039	0.060	0.050	0.027
Sardinian	0.052	0.044	0.044	0.058	0.044	0.038
Scheinfelder	0.053	0.045	0.059	0.070	0.058	0.050
Schoenhengster	0.046	0.044	0.024	0.047	0.030	0.029
Holland Black Pied	0.045	0.039	0.030	0.039	0.031	0.031
Andalusian Black	0.039	0.030	0.036	0.054	0.044	0.027
Scottish Highland	0.044	0.033	0.043	0.049	0.046	0.031
South Devon	0.043	0.033	0.036	0.051	0.044	0.026
Spanish Fighting Cattle	0.040	0.039	0.048	0.062	0.052	0.034
Buchara Grey	0.039	0.035	0.046	0.053	0.056	0.037
Kalmuek Steppe		0.028	0.046	0.055	0.050	0.035
Hungarian Grey	0.028		0.041	0.051	0.046	0.035
Sudeten	0.046	0.041		0.038	0.027	0.025
Sudeten X Tesstal?	0.055	0.051	0.038		0.043	0.042
Tarentaise	0.050	0.046	0.027	0.043		0.036
Telemark	0.035	0.035	0.025	0.042	0.036	
Tesstal	0.042	0.037	0.028	0.035	0.028	0.032
Tudanca	0.041	0.034	0.044	0.064	0.051	0.036
Tuxer	0.094	0.092	0.069	0.076	0.063	0.086
Heck	0.051	0.043	0.058	0.066	0.061	0.051
Niata	0.129	0.130	0.118	0.113	0.102	0.123
Vogtlaender	0.062	0.060	0.037	0.044	0.026	0.047
Walchshofer	0.052	0.045	0.064	0.061	0.071	0.050

Watussi	0.043	0.046	0.048	0.060	0.048	0.040
Zebu	0.047	0.043	0.039	0.056	0.037	0.033
Zebu (India)	0.039	0.034	0.042	0.059	0.044	0.033
Zillertaler	0.069	0.062	0.041	0.049	0.034	0.048
	Tesstal	Tudanca	Tuxer	Heck	Niata	Vogtlaender
Ayrshire	0.031	0.034	0.084	0.050	0.121	0.046
Blondvieh: Carinthian	0.030	0.030	0.085	0.039	0.131	0.052
Blondvieh: Lavanttaler	0.031	0.039	0.086	0.043	0.134	0.055
Blondvieh: Mariahofer	0.030	0.054	0.075	0.064	0.103	0.034
Blondvieh: Murbodner	0.025	0.032	0.083	0.042	0.126	0.050
Blondvieh: Waldviertler	0.032	0.037	0.081	0.055	0.119	0.045
Bos primigenius (Aurochs)	0.080	0.056	0.141	0.056	0.179	0.106
Montafon	0.042	0.043	0.096	0.058	0.123	0.056
Buša	0.035	0.034	0.092	0.047	0.130	0.058
Devon	0.024	0.038	0.078	0.049	0.115	0.038
Egerlaender	0.026	0.042	0.074	0.054	0.116	0.039
Bern Red Pied	0.042	0.030	0.093	0.034	0.134	0.062
Simmental	0.028	0.032	0.082	0.037	0.124	0.048
South Moravian Red Pied	0.032	0.036	0.088	0.050	0.118	0.049
Rubia Gallega	0.048	0.038	0.110	0.049	0.140	0.072
Krainer Grey	0.037	0.040	0.083	0.045	0.135	0.055
Oberinntaler Grey	0.041	0.048	0.086	0.064	0.110	0.046
Guernsey	0.035	0.049	0.078	0.059	0.115	0.043
Iceland	0.036	0.041	0.096	0.051	0.126	0.057
Jersey	0.037	0.065	0.065	0.074	0.097	0.028
Kampeten: Styrian Bergscheck	0.026	0.036	0.077	0.052	0.119	0.041
Kampeten: Welser Schecken	0.041	0.022	0.099	0.035	0.142	0.065
Kerry	0.033	0.029	0.086	0.049	0.126	0.050
Cretan	0.061	0.043	0.117	0.054	0.144	0.081
Kuhlaender	0.025	0.047	0.067	0.052	0.113	0.034
Limousin	0.022	0.047	0.072	0.051	0.110	0.035
Moravian Landschlag	0.026	0.048	0.069	0.052	0.119	0.038
Normande	0.040	0.057	0.076	0.069	0.094	0.033
North Wales	0.025	0.040	0.079	0.045	0.124	0.044
White Park	0.047	0.056	0.090	0.060	0.117	0.053
Pasiega	0.056	0.045	0.103	0.049	0.139	0.068
Pinzgauer	0.022	0.051	0.058	0.056	0.112	0.030
Pinzgauer: Moelltaler	0.027	0.044	0.076	0.048	0.113	0.042
Pirenaica	0.026	0.045	0.079	0.055	0.115	0.038
Maas-Rhein-Ijsselschlag	0.027	0.033	0.085	0.044	0.120	0.046
Danish Red	0.034	0.033	0.088	0.046	0.130	0.052
Angeln	0.025	0.046	0.081	0.049	0.119	0.048
Bohemian Red	0.032	0.029	0.088	0.045	0.129	0.051
Polish Red	0.043	0.036	0.099	0.056	0.135	0.064
Sardinian	0.044	0.038	0.098	0.044	0.133	0.060
Scheinfelder	0.052	0.040	0.108	0.033	0.148	0.074
Schoenhengster	0.031	0.041	0.073	0.052	0.122	0.041

Holland Black Pied	0.024	0.042	0.075	0.045	0.120	0.042
Andalusian Black	0.041	0.030	0.099	0.047	0.135	0.062
Scottish Highland	0.038	0.033	0.097	0.033	0.132	0.060
South Devon	0.037	0.035	0.094	0.051	0.130	0.056
Spanish Fighting Cattle	0.047	0.036	0.105	0.044	0.144	0.068
Buchara Grey	0.040	0.042	0.100	0.040	0.144	0.066
Kalmuek Steppe	0.042	0.041	0.094	0.051	0.129	0.062
Hungarian Grey	0.037	0.034	0.092	0.043	0.130	0.060
Sudeten	0.028	0.044	0.069	0.058	0.118	0.037
Sudeten X Tesstal?	0.035	0.064	0.076	0.066	0.113	0.044
Tarentaise	0.028	0.051	0.063	0.061	0.102	0.026
Telemark	0.032	0.036	0.086	0.051	0.123	0.047
Tesstal		0.047	0.071	0.052	0.116	0.038
Tudanca	0.047		0.099	0.033	0.142	0.069
Tuxer	0.071	0.099		0.104	0.096	0.049
Heck	0.052	0.033	0.104		0.151	0.076
Niata	0.116	0.142	0.096	0.151		0.090
Vogtlaender	0.038	0.069	0.049	0.076	0.090	
Walchshofer	0.060	0.052	0.122	0.053	0.149	0.083
Watussi	0.053	0.048	0.085	0.052	0.125	0.056
Zebu	0.037	0.035	0.092	0.045	0.128	0.055
Zebu (India)	0.042	0.031	0.098	0.049	0.126	0.061
Zillertaler	0.043	0.062	0.063	0.063	0.106	0.036
	Walchshofer	Watussi	Zebu	Zebu (India)	Zillertaler	
Ayrshire	0.050	0.038	0.028	0.031	0.048	
Blondvieh: Carinthian	0.049	0.042	0.031	0.037	0.048	
Blondvieh: Lavanttaler	0.057	0.061	0.032	0.038	0.048	
Blondvieh: Mariahofer	0.064	0.054	0.039	0.042	0.039	
Blondvieh: Murbodner	0.051	0.044	0.034	0.034	0.052	
Blondvieh: Waldviertler	0.057	0.050	0.034	0.033	0.045	
Bos primigenius (Aurochs)	0.056	0.077	0.066	0.065	0.100	
Montafon	0.049	0.049	0.033	0.032	0.057	
Buša	0.057	0.051	0.028	0.030	0.055	
Devon	0.050	0.043	0.032	0.032	0.041	
Egerlaender	0.061	0.050	0.035	0.037	0.041	
Bern Red Pied	0.052	0.044	0.041	0.041	0.061	
Simmental	0.049	0.040	0.029	0.033	0.045	
South Moravian Red Pied	0.047	0.042	0.036	0.028	0.052	
Rubia Gallega	0.029	0.052	0.045	0.038	0.073	
Krainer Grey	0.053	0.042	0.049	0.050	0.054	
Oberinntaler Grey	0.056	0.047	0.039	0.035	0.052	
Guernsey	0.062	0.045	0.044	0.045	0.047	
Iceland	0.046	0.051	0.031	0.034	0.052	
Jersey	0.072	0.058	0.051	0.054	0.038	

Kampeten: Styrian Bergscheck	0.057	0.044	0.030	0.034	0.044	
Kampeten: Welser Schecken	0.046	0.051	0.031	0.033	0.059	
Kerry	0.049	0.043	0.031	0.027	0.051	
Cretan	0.047	0.050	0.048	0.044	0.081	
Kuhlaender	0.061	0.044	0.039	0.044	0.040	
Limousin	0.058	0.049	0.037	0.042	0.032	
Moravian Landschlag	0.059	0.043	0.039	0.049	0.040	
Normande	0.066	0.053	0.046	0.045	0.042	
North Wales	0.052	0.044	0.035	0.041	0.043	
White Park	0.072	0.059	0.037	0.048	0.040	
Pasiega	0.050	0.049	0.050	0.054	0.060	
Pinzgauer	0.067	0.048	0.045	0.051	0.036	
Pinzgauer: Moelltaler	0.054	0.046	0.038	0.040	0.042	
Pirenaica	0.051	0.046	0.035	0.037	0.040	
Maas-Rhein-Ijsselschlag	0.047	0.039	0.028	0.031	0.046	
Danish Red	0.051	0.049	0.034	0.036	0.048	
Angeln	0.056	0.057	0.039	0.038	0.047	
Bohemian Red	0.048	0.046	0.029	0.028	0.049	
Polish Red	0.049	0.052	0.044	0.033	0.066	
Sardinian	0.045	0.049	0.036	0.040	0.055	
Scheinfelder	0.048	0.056	0.044	0.049	0.065	
Schoenhengster	0.064	0.045	0.039	0.042	0.042	
Holland Black Pied	0.061	0.047	0.035	0.042	0.040	
Andalusian Black	0.041	0.049	0.036	0.030	0.061	
Scottish Highland	0.037	0.043	0.033	0.037	0.052	
South Devon	0.045	0.050	0.038	0.034	0.058	
Spanish Fighting Cattle	0.045	0.047	0.040	0.040	0.068	
Buchara Grey	0.043	0.051	0.046	0.048	0.065	
Kalmuek Steppe	0.052	0.043	0.047	0.039	0.069	
Hungarian Grey	0.045	0.046	0.043	0.034	0.062	
Sudeten	0.064	0.048	0.039	0.042	0.041	
Sudeten X Tesstal?	0.061	0.060	0.056	0.059	0.049	
Tarentaise	0.071	0.048	0.037	0.044	0.034	
Telemark	0.050	0.040	0.033	0.033	0.048	
Tesstal	0.060	0.053	0.037	0.042	0.043	
Tudanca	0.052	0.048	0.035	0.031	0.062	
Tuxer	0.122	0.085	0.092	0.098	0.063	
Heck	0.053	0.052	0.045	0.049	0.063	
Niata	0.149	0.125	0.128	0.126	0.106	
Vogtlaender	0.083	0.056	0.055	0.061	0.036	
Walchshofer		0.065	0.057	0.050	0.080	
Watussi	0.065		0.051	0.056	0.059	

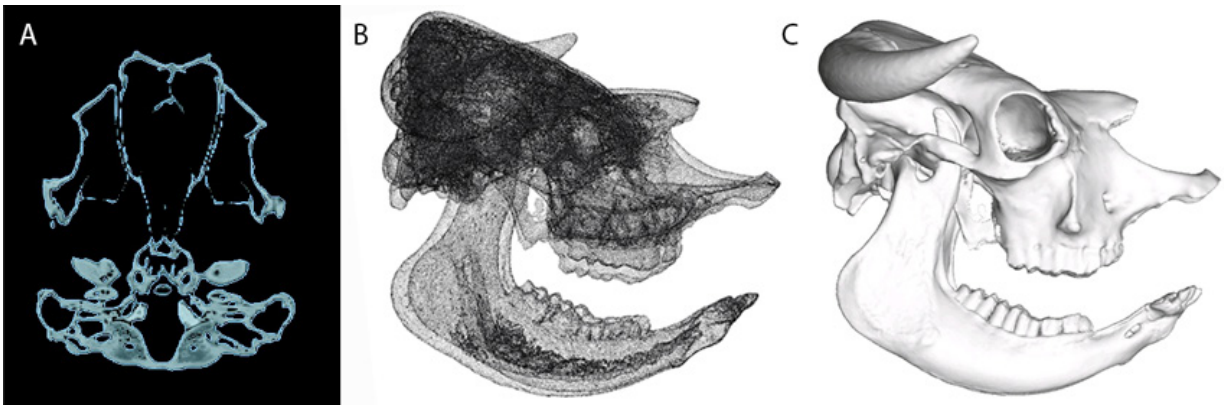
Zebu	0.057	0.051		0.031	0.047	
Zebu (India)	0.050	0.056	0.031		0.059	
Zillertaler	0.080	0.059	0.047	0.059		

Finite Element Analysis

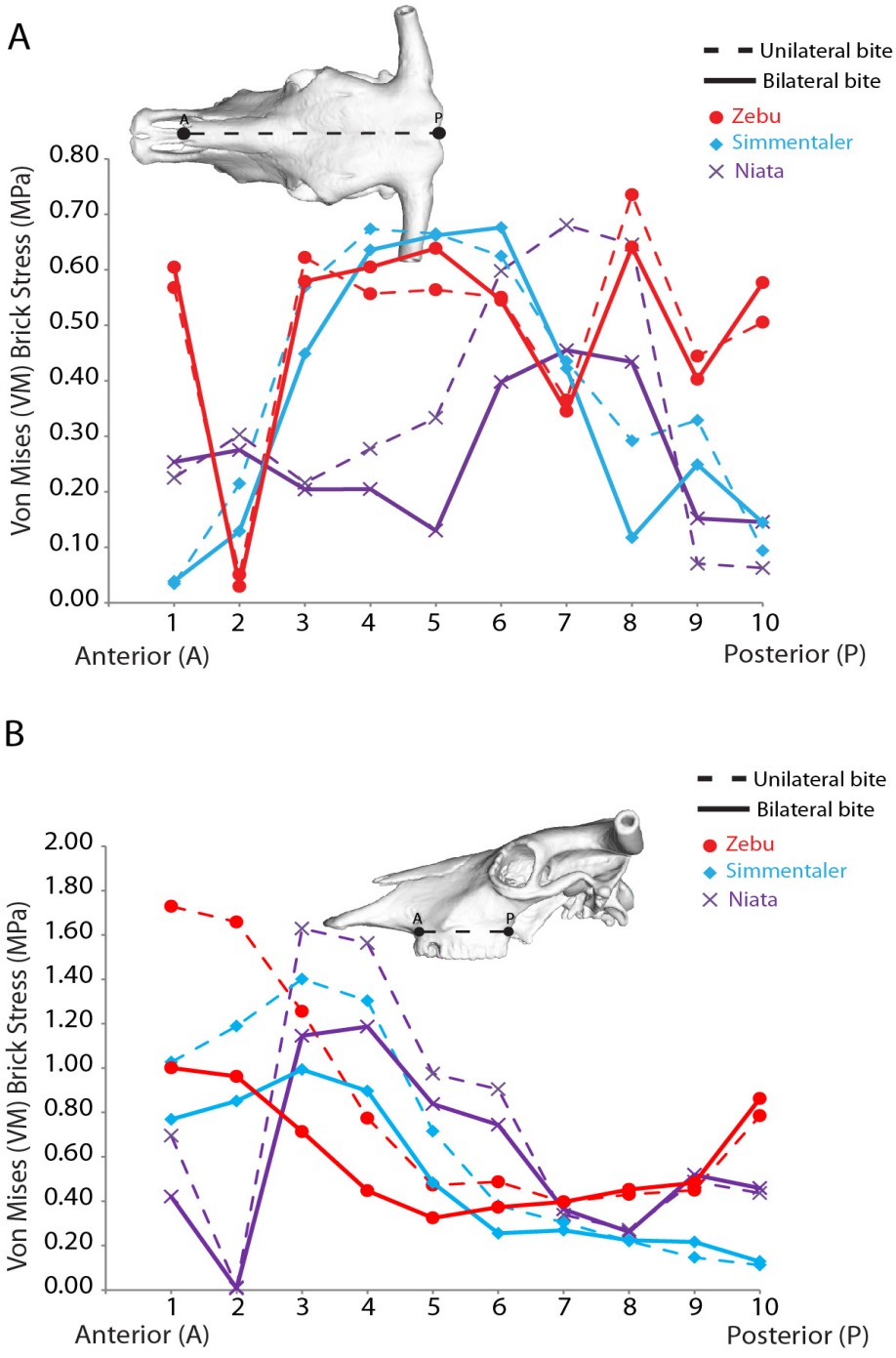
Further comparison on the FEA analysis

The contour maps of VM stress in dorsal view indicated that, for both loading case simulations (unilateral molar bite at M2, anterior bilateral bite at M1), the Zebu crani-um displayed high stress levels when compared to the Niata and Simmentaler. The frontal and nasal bones experienced comparatively more stress in the Zebu, espe-cially along the midline compared to the other breeds (Figure 5, dorsal models G,I,K). For all loading cases in lateral view, the Zebu showed greater VM stress extending across the frontal and maxilla than did the Simmentaler and Niata, and especially towards the suture between the maxilla and zygomatic in both loading cases (Figure 5, A-F).

The Zebu showed markedly higher VM stress (average = 0.59 MPa) at the most an-terior point of the nasal and at the most posterior point sampled (average = 0.55 MPa), compared to the values for the Simmentaler (point 1, average = 0.04 MPa; point 10, average = 0.12 MPa) and Niata (point 1, average = 0.24 MPa; point 10, av-erage = 0.11 MPa).



Supplementary Figure 11: Creating virtual models for Finite Element Analysis (FEA): (A) thresholding of computed tomography (CT) image slices, seen in axial view; (B) generation of a volume mesh following remeshing of surface mesh using controlled geometric error and triangle edge length values; (C) assembly of a Finite Element Model (FEM) in Strand 7. Model shown is for the Niata breed, specimen MLP 1126.



Supplementary Figure 12: Von Mises stress plots: VM stress values were extracted at 10 equidistant points from anterior to posterior along the mid-saggital plane (A) and margin of the tooth row (B) for each model under loading conditions simulating an anterior bilateral bite (solid line) and an anterior unilateral bite (dashed line).

Supplementary Table 11: Muscle forces used for each jaw muscle group in un-scaled intrinsic models. Muscle forces were calculated using muscle mass propor-tions following the 'dry skull' method, where maximum cross-sectional area (CSA) was calculated for each muscle group [1]. Muscle forces were scaled relative to body mass for each specimen following a 2/3 power relationship, whereby muscle force is proportional to cross-sectional area whereas body mass is proportional to volume [2]. MLP 1126 was used as the target (=reference) specimen for scaling.

Jaw muscle group	Muscle force (Newtons) per jaw muscle group (one side)		
	Niata (MLP 1126)	Simmentaler (17765)	Zebu (17767)
m. masseter	1434.59	2304.43	2178.16
m. temporalis	957.98	1538.82	1454.51
m. pterygoideus lateralis	309.32	496.87	469.64
m. pterygoideus medialis	889.87	1429.42	1351.11
TOTAL	3951.75	5769.54	5453.42
Scaled muscle force	1	1.46	1.38

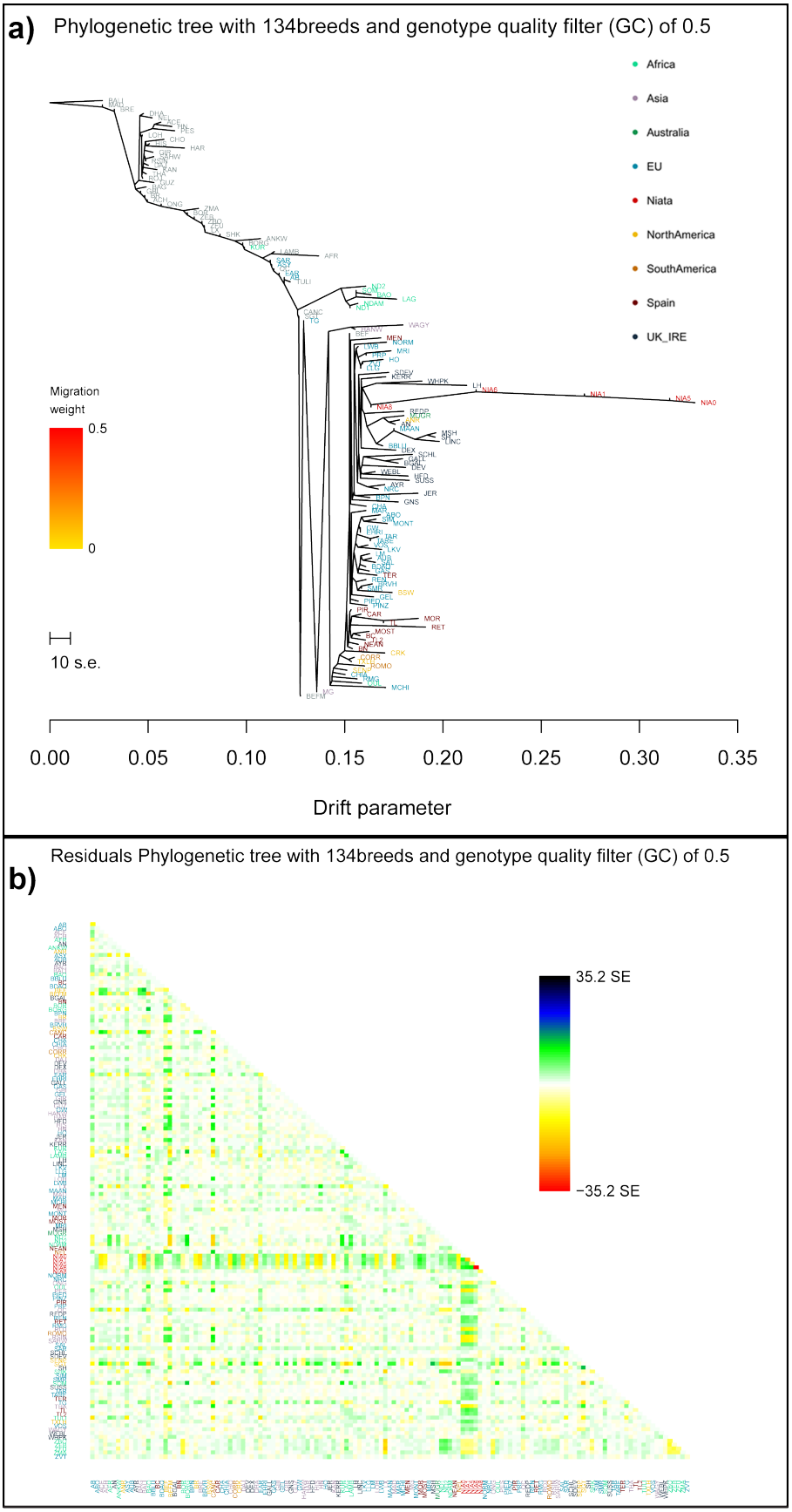
Supplementary Table 12: Strain results for simulated anterior unilateral bite cases. Values for Maximum Principal (=Max Prin) strain, Minimum Principal (=Min Prin) strain, absolute value of Max Prin/Min Prin (=Mode), and Von Mises strain recorded at the temporomandibular joint (TMJ).

Location	Specimen	Max Prin (με)	Min Prin (με)	Mode	Von Mises (με)
Working-side TMJ	Niata (MLP 1126)	112.79	-139.52	0.81	218.76
	Simmentaler (17765)	239.44	-95.88	2.5	318.61
	Zebu (17767)	250.88	-162.25	1.55	383.86
Balancing-side	Niata (MLP 1126)	62.65	-181.99	0.34	218.05
TMJ					
	Simmentaler (17765)	176.27	-206.27	0.85	338.81
	Zebu (17767)	139.6	-341.01	0.41	424.2

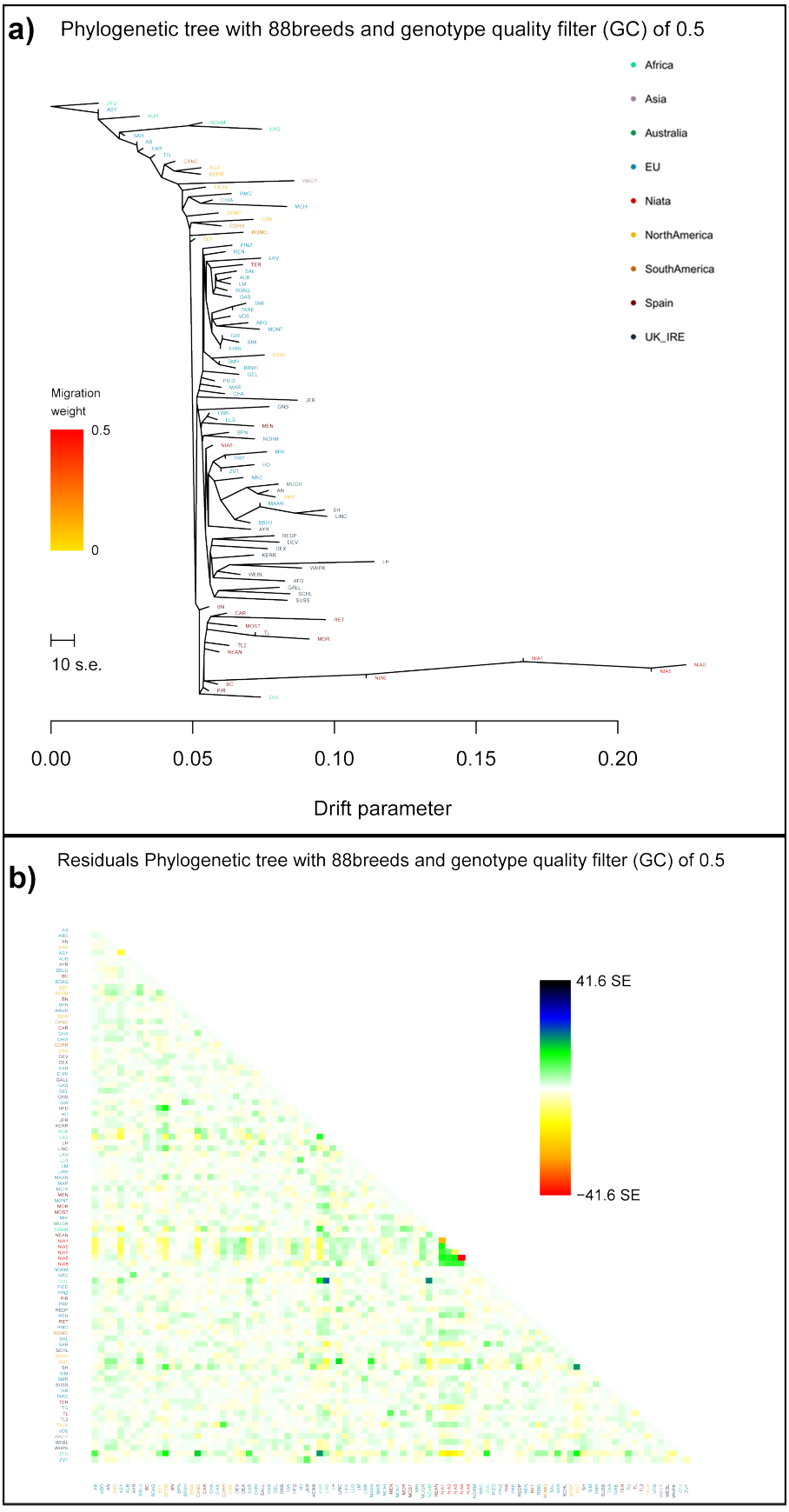
References

1. Thomason JJ (1991). Cranial strength in relation to estimated biting forces in some mammals. Can J Zool. 69(9):2326-33.
2. Wroe S, Chamoli U, Parr WCH, Clausen P, Ridgely R, Witmer L (2013). Comparative Biomechanical Modeling of Metatherian and Placental Saber-Tooths: A Different Kind of Bite for an Extreme Pouched Predator. PLoS ONE. 8(6):e66888.

Genetic Analysis



Supplementary Figure 13: a) Phylogenetic tree with 134 breeds and 5 Niata samples of GC ≥ 0,5. b) Residuals.



Supplementary Figure 14: a) Phylogenetic tree with 88 breeds and 5 Niata samples of GC ≥ 0,5. b) Residuals.

Body size data

Supplementary Table 13: Body sizes of taurine cattle breeds as published by Felius [1] and Niata.

Breed	Medium Steer weight (kg)	Medium Steer height (cm)	Medium Cow weight (kg)	Medium Cow height (cm)
Aberdeen-Angus	1000	135	650	125
Abondance	1000	147	600	133
Agerolese	650	135	450	125
Akshi	-	135	200	105
Ala Tau	900	-	485	130
Alberes	362.5	-	285	125
Algerian Guelma	400	125	250	115
Alistana-Sanabresa	800	150.5	575	142
Anatolian Black	-	-	225	107.5
Andalusian Black	812.5	140	550	135
Angeln	975	145.5	560	131
Aosta Black Pied	600	130	500	125
Aosta Red Pied	650	132.5	500	130
Apulian Podolian	700	152.5	405	127.5
Argentine Criollo	700	160	450	135
Argentine Criollo (Fronterizo)	-	-	325	135
Arouquesa	660	134	405	123
Asturian Mountain	675	132.5	450	122.5
Asturian Valley	1000	147.5	700	135
Aubrac	825	140	580	130
Aulie Ata	885	140	495	130
Aure et St Girons	-	-	600	135
Aurochs (*Bos primigenius*)	800	180	600	160
Austrian Pinzgauer	1000	143.5	650	134
Avilena-Black Iberian	825	145	550	138
Ayrshire	700	140	550	131
Baoule	265	105	175	95
Barrosa	625	127.5	367.5	118.5
Barroso	812.5	150	450	135
Bazadais	1050	145	700	135
Beef Shorthorn	1025	145	650	135
Belgian Red	1200	153	687.5	138
Belgian White and Red	1350	155	750	138
Belgian White Blue	1275	151.5	750	132.5
Bérnais	-	130	550	125
Berrenda Black Pied	900	143	575	138
Berrenda Red Pied	900	143	575	138
Bestuzhev	870	140	520	130
Black Pied Dairy Cattle	-	-	600	135
Blacksided Trondheim and Nordland	850	-	445	117
Blonde d'Aquitaine	1400	160	950	150

Bohemian Red	-	-	500	125
Brazilian Polled	750	132	420	130
Breton Black Pied	650	123	450	117
British White	850	120	575	110
Burlina	625	130	525	120
Byelorus Red	750	135	460	130
Cabannina	550	125	375	120
Cachena	412.5	122	265	100
Caldelana	675	132	450	128
Calvana	1025	157.5	700	147.5
Camargue	437.5	130	304.5	120
Canary Island	900	152	575	148
Carinthian Blond	825	140	550	132.5
Caucasian Brown	780	-	485	126.5
Cauyen Red	855	138	450	125
Chaco Criollo	-	-	500	155
Charolais	1425	145	975	135
Chianina	1215	167.5	900	155
Chillingham	300	-	280	110
Chinese Black and White	1020	150	562.5	135
Cinesara	650	145	475	135
Corsican	450	130	340	115
Croatian Busa	-	-	215	111
Czech Pied	1300	150	700	140
Dairy Shorthorn	1200	150	675	140
Dalmatian Grey	-	-	275	122
Danish Jersey	-	-	450	120
Danish Red	925	154	637.5	137
Devon	1000	-	500	130
Dexter	450	95	300	95
Donnersberg Red	1106	150	625	138
Doran	500	-	350	120
Dutch Black Pied (Holstein-Friesian)	1100	165	750	150
East Finncattle	600	135	440	118
East German Black Pied Cattle	1000	140	650	130
Estonian Black Pied	900	138	500	128
Estonian Native	800	134	520	125
Estonian Red	850	135	500	128
Ferrandais	-	-	650	138
Fighting Cattle	650	127.5	350	115
Forest Muturu	-	-	200	89
Froment du Léon	-	-	550	135
Fuzhou	765	138	415	130
Gacko	-	-	300	117
Galician Blond	1000	145	650	135
Galloway	750	135	520	120

Garfagnina	600	140	425	125
Gascon	850	145	550	135
Gelbvieh	1200	152	750	140
German Original Black Pied	900	155	600	136
German Pinzgauer	900	137	700	135
German Red Pied	1300	150	700	137
German-Angus	1100	142.5	625	132.5
Ghana Shorthorn	-	-	185	88
Glan cattle	1000	148	650	140
Gloucester	750	130	562.5	125
Golpayegani	-	-	230	110
Gorbatov Red	830	133	480	122
Greater Caucasus	-	-	250	104
Greek Shorthorn	-	-	275	107
Greek Steppe	400	123	265	112.5
Grey Alpine	950	133	575	126
Groningen Whiteheaded	-	-	600	137.5
Guernsey	800	152	500	137
Guinean N‘Dama	305	118	255	112
Harz Red	1100	150	600	135
Hazake	435	120	300	110
Heckrind	600	135	-	125
Hereford	1100	152	700	140
Hérens	775	128	610	123
Highland	700	128	470	115
Hinterwald	775	132.5	415	119
Holstein	1125	175	850	155
Hungarian Grey Steppe	750	150	535	138
Icelandic Dairy Cattle	-	-	425	130
Iskar	750	140	400	118
Istoben	755	-	440	127.5
Istrian	825	148	585	137.5
Japanese Black	825	135	517.5	125
Japanese Brown	950	143	600	130
Japanese Shorthorn	950	142	660	128
Jaulan	-	-	350	114
Jersey	550	127	387.5	117.5
Kalmyk	750	137	537.5	127.5
Kapsiki	380	115	230	110
Kazakh	500	130	272.5	115
Kazakh Whiteheaded	825	-	530	134
Kerry	590	140	375	122
Kholmogory	885	145	580	132.5
Kolubara	550	-	380	124
Korean Native	460	135	370	125
Kostroma	850	140	520	132
Kurgan	850	140	535	130

Lages Criollo	-	140	475	127
Lagune	-	95	155	85
Lakenvelder	700	137	550	132
Latvian Brown	800	140	455	130
Lebedin	900	142	575	133
Leonese	650	136	500	130
Liberian Dwarf	-	-	120	90
Libyan Shorthorn	380	120	290	110
Limousin	1200	145	700	137
Limpurger	1000	145	625	135
Lithuanian Black Pied	950	140	550	129
Lithuanian Red	750	135	490	126
Longhorn	1000	150	850	135
Lourdais	-	-	525	135
Luing	900	138.5	-	-
Maine-Anjou	1259	152	850	142
Marchigiana	1300	157.5	800	145
Maremmana	900	155	600	145
Marinhoa	875	150	585	140
Maronesa	600	140	375	130
Menorcan	850	144	612.5	138
Meuse-Rhine-Yssel	1100	150	600	135
Middle German Red	-	-	625	130
Mingrelian Red	465	-	300	112.5
Mirandais	750	130	450	120
Mirandesa Beiroa	950	147.5	575	137.5
Mishima	450	123	280	112.5
Modenese	1050	155	650	145
Modicana	925	152.5	505	137.5
Mongolian Gobi	-	-	270	107
Mongolian Halhin Gol	117.5	377.5	360	115
Mongolian Intermediate	-	-	350	110
Montana	700	140	500	130
Montbéliard	1150	148	685	137.5
Moroccon Brown Atlas	375	135	300	115
Morucha	750	145	475	140
Mostrenca	900	145	550	135
Murboden	900	145	600	135
Murcian	850	140	575	132.5
Murnau-Werdenfels	925	138	550	128
Namchi	200	103	186	99
Niata	430	130	-	-
Normande	1100	152	750	140
North Finncattle	550	128	350	112.5
Northern Blue	1050	148	725	135
Norwegian Red	1000	142	575	130
Original Allgäu	900	145	550	135

Oropa	850	135	625	125
Oulmes-zaer	450	135	325	120
Palmera	850	138	487.5	133
Parthenais	1075	142.5	725	135
Piedmont	900	150	600	145
Pirenaica	950	140	575	132.5
Pisana	815	160	525	147.5
Polish Black-and-White Low-land	650	132	550	128
Polish Red Highland	775	135	465	122.5
Pontremolese	750	145	475	128
Posavina	600	-	300	120
Pustertal	800	138.5	500	129
Red Flemish	1100	148	675	140
Red Poll	750	145	525	129.5
Red Polled Eastland	775	140	475	123
Red Steppe	900	139	500	128.5
Reggiana	650	150	450	140
Rendena	600	130	475	125
Retinta	825	146	540	137.5
Rhaetian Grey Cattle	750	130	450	117.5
Rodopi	350	115	240	95
Romagnola	1150	145	800	135
Romanian Brown	1050	142	550	128
Romanian Mountain	-	-	215	104
Romanian Simmental	1040	148	600	135
Romanian Steppe	600	130	300	118
Romosinuano	650	135	550	130
Russian Swiss	850	139	500	131
Salers	975	150	700	140
San Martinero	800	135	475	130
Sanhe	1050	157.5	697.5	132.5
Sardinian	290	105	250	102.5
Sardo-Modicana	600	145	525	135
Sayaguesa	1050	160	650	145
Serrano	-	-	500	140
Shetland	-	-	290	105
Slovakian Pied	1050	145	650	135
Slovakian-Carpathian Brown	800	-	450	125
Slovanian Steppe	-	-	465	127
Slovenian and Croatian Simm-ental	1150	152	575	137
Slowakian Pinzgauer	850	136	550	128
Slowenian/Yugoslavian Brown	1100	152	600	134
Somba	205	-	160	94.5
South and West Norwegian	812.5	136	475	117
South Devon	1250	155	675	138
Suksun	920	-	390	130

Sussex	950	150	600	140
Swedish Mountain	590	130	395	120
Swedish Red -and-White	975	135	600	130
Swedish Red Polled	650	130	400	120
Swiss Brown	1087.5	150	675	137.5
Swiss Simmental	1300	154	800	141
Sychevka	1050	146	630	133
Tagil	887.5	-	480	130
Tambov Red	700	136	460	127
Tarentaise	800	140	575	127
Telemark	825	-	400	120
Texas Longhorn	670	130	400	120
Tibetan	215	105	200	100
Transylvanian Pinzgauer	900	134	450	127
Tudanca	540	135	370	130
Turkish Brown	-	-	600	140
Turkish Grey Steppe	400	-	340	120
Tux-Zillertal	-	-	550	125
Tyrol Grey	950	137.5	570	127.5
Ukrainian Polish Red	750	135	465	125
Ukrainian Steppe	800	137	525	129
Ukrainian Whiteheaded	750	136	425	128
Urkainian-Carpathian Brown	910	137	490	128
Vianesa	850	138.5	525	135
Villard-de-Lans	-	-	600	140
Vogelsberg Cattle	600	138	500	128
Vorderwald	975	148	625	132.5
Vosges	700	142.5	500	130
Waldviertler Blond	900	140	575	132
Welsh Black	1000	145	675	130
West Finncattle	737.5	140	470	123
Westphalian Red	1100	150	650	135
White park	955	-	542.5	130
Xinjiang Brown	760	137	432.5	121.5
Yakut	525	122	375	111
Yanbien	467.5	130	365	120
Yaroslavl	822	-	480	128
Yugoslavian Busa	405	117.5	200	105
Yurino	775	132	490	122.5

References

1. Felius M (1995). Cattle breeds: an encyclopedia. Doetinchem: Misset.

Conclusions and Future Perspectives

The presented thesis compiles several case studies with the aim to investigate life history evolution and disparity within Laurasiatheria. The selection of the particular group of interest followed the principle of suitability for a particular question at hand. In summary, this thesis used skulls, lower jaws, and femora to investigate life history variables in extant and extinct Cervidae and Ursidae. Additionally, the effect of artificial selection on cattle was examined based on the case of the Niata cattle from South America. The results show that the broad life history implications of the Schultz rule [1] are not met within Cervidae and that the observed variation in tooth replacement and eruption sequences result from several heterochronic shifts within the phylogenetic history of Cervidae. A resulting ancestral stage was supported by evidence from the fossil record. By investigating brain size, it became evident that cave bears had a small brain for their body size. This was potentially caused by shifts in its ecology compared to other extant bear species. Brain size in carnivorans is associated with several life history variables [2]. Thus, it can be hypothesized that cave bears gave birth to many, small cubs after long gestation. Additionally, weaning mass was small. Some of these implications are supported by observations based on bone histology. Cave bears were fast growing, comparable to polar bears, but reached skeletal maturity late in life. Still, fast growth indicates early maturity [3] and might, in this case, indicate sexual maturity rather than skeletal one. The example of the cave bears illustrates that bones can be used to reconstruct the complex nature of life history of extinct animals. By investigating the process of domestication in the case of the Niata cattle, the extent of morphological variation within cattle was quantified and statements made by Darwin [4] were investigated for the first time.

To conclude, this thesis presents evidence about the potential and limitations in reconstructing crucial events in the life of an animal based on skeletal remains. Some events are conserved in phylogeny and thus are not suitable to infer life history implications, whereas others are powerful tools able to directly or indirectly shed light on growth and maturity in Laurasiatheria. Additionally, the study of domesticated animals gives crucial insights into limitations of intraspecific variability.

There are many directions for future applications of the presented work. For example, in Carnivora tooth eruption patterns are not well understood and the reduction of teeth in the evolution of several lineages complicates standardization. Nonetheless, finding new approaches to investigate tooth eruption in these animals will provide further crucial evidence on the extent of life history implications of relative eruption sequences. Additionally, standardized comparative studies on the growth of mammals based on bone histology are still in their infancy and many species still need to be examined [5]. These are just two examples, however, the overall study of variability, disparity, and life history evolution in mammals is

a wide field with many unanswered questions for future scientific endeavours.

References

1. Smith HB (2000). 'Schultz's Rule' and the evolution of tooth emergence and replacement patterns in primates and ungulates. New York: Cambridge University Press.
2. Finarelli JA (2010). Does encephalization correlate with life history or metabolic rate in Carnivora? Biol Lett. 6(3):350-3.
3. Stearns SC (2000). Life history evolution: successes, limitations, and prospects. Naturwissenschaften. 87(11):476-86.
4. Darwin C (1845). Journal of researches into the geology and natural history of the various countries visited by H.M.S. Beagle round the world, under the Command of Capt. Fitz Roy, R.N. 2nd edition. London: John Murray.
5. Kolb C, Scheyer TM, Veitschegger K, Forasiepi AM, Amson E, Van der Geer AAE, Van den Hoek Ostende L, Hayashi S, Sánchez-Villagra MR (2015). Mammalian bone palaeohistology: a survey and new data with emphasis on island forms. PeerJ. 3:e1358.

APPENDIX I

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Book review

Hypsodonty in Mammals—Evolution, Geomorphology, and the Role of Earth Surface Processes, Richard H. Madden, Cambridge University Press, (2015). $130.00, 423 pp. ISBN 978-1-107-01293-6

Hypsodonty in Mammals is Richard H. Madden's successful attempt to explore the consequences of the ingestion of soil minerals and the effect of earth surface processes, such as erosion, in the evolution of hypsodonty, a morphological condition that refers to teeth with high crowns providing more material to wear down in a high abrasive diet and environment. Some mammal lineages developed ever-growing teeth (elodonty), which means that the roots never close enabling the teeth to grow constantly during their life span. The appearance of such features in e.g. ungulates has been traditionally linked with the expansion of grasslands and environmental changes during the Miocene (e.g., Damuth and Janis, 2011; Mihlbachler et al., 2011). The fossil record of South American mammals shows a particular case of "precocious hypsodonty". On this continent, a large number of mammal species developed high-crowned teeth already during the Eocene, before grasses became a dominant floral element. With this book Madden proposes soil ingestion as a major factor in the development of hypsodonty. The author uses data from different disciplines such as sedimentology, island biogeography, and paleontology to achieve an integrative view on this topic. He compiled a well-rounded synthesis and presents an interdisciplinary book that brings together different data into a coherent argument. As the author points out, "the central idea of this book is stronger than the sum of its individual parts."

The book is divided into 10 chapters. In the first three chapters the reader is introduced to the fossil record, geological history, and extant fauna of the South American continent. Madden discusses the origins of the hypothesis that soil ingestion might drive the evolution of hypsodonty and gives its historical background. The first chapter gives the general context and sets up the questions addressed in the book. It provides an introduction to phytoliths (hard silica particles in some plant tissues) and how abrasive soil can be ingested with the diet of an animal. The second chapter develops the particular case of precocious hypsodonty in South American mammals. In chapter three, Madden presents an overview of the prevalence of hypsodonty in extant South American mammals at a continental scale, and gives a global view of the evolution of high-crowned teeth.

In the fourth chapter the reader now leaves the South American continent and explores evidence for the influence of earth surface processes on tooth wear in a detailed case study of sheep in New Zealand. Here, European settlers observed that their sheep had to be culled prematurely due to excessive tooth wear. Madden reviews the literature on this phenomenon and compares areas with different soil properties to present a case of excessive tooth wear due to soil ingestion. Traveling north from New Zealand, the fifth chapter explores data from Australia. Kangaroos are among the dominant herbivores of this landmass but have not developed hypsodonty, seemingly due to constraints (Janis, 1989). Madden collected data on tooth wear in sheep, dust storms as well as the crown height of aboriginal people and incorporates these well into his synthesis.

The sixth chapter explores past and present cases of hypsodonty and extensive tooth wear on islands, which are classic models to study morphological changes because of the high evolutionary rates recorded there. The reader is introduced to the fossil record of different Mediterranean islands and the evolution of hypsodonty and elodonty in some former inhabitants such as the extinct goat *Myotragus*. In historical times, the settlers introduced domesticated animals to different regions which provides a rich subject of study. Goats and sheep were introduced to islands with different soil structure all over the world. Some of these islands, however, have similar climate and vegetation and therefore represent a good source of data to compare tooth wear patterns. Madden studies differences in tooth wear between caprine species from volcanic islands and islands with less abrasive soils. The next two chapters aim to test the hypothesis in geologic time using the fossil record. Chapter seven explores hypsodonty in the East African rift valley, looking at early hominids and suids. Here, Madden presents the way these two phylogenetically distant bunodont mammal groups responded to environmental change. The eighth chapter brings the reader back to Patagonia in South America. The fossil record is explored in the light of the new evidence and arguments developed through the book. The changes in the fossil record are compared with data on paleoclimate, soil structure changes, and vegetation. Chapter nine elaborates on the anatomy and evolution of elodonty. It explores its origin, its advantages, and its capacity to modify the landscape. Madden uses, among others, the vicugna and rabbits as model examples. The last chapter is a useful summary of the book.

This book presents the result of a lifelong commitment to the study of hypsodonty in mammals and is an excellent example for illustrating the complexity of evolutionary changes and processes and how organisms interact with the environment. Madden's work highlights the importance to go outdoors and experience nature by ourselves in order to understand these complex evolutionary processes. With this book, Madden summarizes and develops a hypothesis for dental evolution, which can now be tested by more empirical data from a variety of disciplines, providing an exciting avenue of research for many young scientists. In summary, Hypsodonty in Mammals not only offers the reader an extensive amount of data but also a source of inspiration for future scientific endeavours.

References

Damuth, J., Janis, C.M., 2011. On the relationship between hypsodonty and feeding ecology in ungulate mammals, and its utility in palaeoecology. Biol. Rev. 86, 733–758.

http://dx.doi.org/10.1016/j.mambio.2016.02.007
1616-5047/

Janis, C.M., 1989. Why kangaroos (*Marsupialia*: *Macropodidae*) are not as hypsodont as ungulates (*Eutheria*). Aust. Mammalogy 13, 49–53.
Mihlbachler, M.C., Rivals, F., Solounias, N., Semprebon, G.M., 2011. Dietary change and evolution of horses in North America. Science 331, 1178–1181.

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APPENDIX II

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Mammalian bone palaeohistology: a survey and new data with emphasis on island forms

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ABSTRACT

The interest in mammalian palaeohistology has increased dramatically in the last two decades. Starting in 1849 via descriptive approaches, it has been demonstrated that bone tissue and vascularisation types correlate with several biological variables such as ontogenetic stage, growth rate, and ecology. Mammalian bone displays a large variety of bone tissues and vascularisation patterns reaching from lamellar or parallel-fibred to fibrolamellar or woven-fibred bone, depending on taxon and individual age. Here we systematically review the knowledge and methods on cynodont and mammalian bone microstructure as well as palaeohistology and discuss potential future research fields and techniques. We present new data on the bone microstructure of two extant marsupial species and of several extinct continental and island placental mammals. Extant marsupials display mainly parallel-fibred primary bone with radial and oblique but mainly longitudinal vascular canals. Three juvenile specimens of the dwarf island hippopotamid *Hippopotamus minor* from the Late Pleistocene of Cyprus show reticular to plexiform fibrolamellar bone. The island murid *Mikrotia magna* from the Late Miocene of Gargano, Italy displays parallel-fibred primary bone with reticular vascularisation and strong remodelling in the middle part of the cortex. *Leithia* sp., the dormouse from the Pleistocene of Sicily, is characterised by a primary bone cortex consisting of lamellar bone and a high amount of compact coarse cancellous bone. The bone cortex of the fossil continental lagomorph *Prolagus oeningensis* and three fossil species of insular *Prolagus* displays mainly parallel-fibred primary bone and reticular, radial as well as longitudinal vascularisation. Typical for large mammals, secondary bone in the giant rhinocerotoid *Paraceratherium* sp. from the Late Oligocene of Turkey is represented by dense Haversian bone. The skeletochronological features of *Sinomegaceros yabei*, a large-sized deer from the Pleistocene of Japan closely related to *Megaloceros*, indicate a high growth rate. These examples and the synthesis of existing data show the potential of bone microstructure to reveal essential information on life history evolution. The bone tissue and the skeletochronological data of the sampled island species suggest

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Appendix III

The role of phylogeny in morphological and developmental studies of animal domestication
(manuscript in preparation)

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Abstract (submitted to BioSyst 2017, Gothenburg)

Current studies of domestication concentrate on genomics and zooarcheological approaches. Investigation of phylogenetically-informed developmental morphology can also provide major insights into evolution, as informed by studies of breeds of domesticated forms and comparisons with wild counterparts. Features of the 'domestication syndrome', a hypothetical set to appear in domesticated forms, do not appear universally across mammalian species, only pigmentation and rostral shortening do. Likewise, ontogenetic trajectories are not equally modified in domesticated forms of all species. The examination of more than 400 skulls across 13 domesticated forms and their wild counterparts serve to quantify and analyse the changes with multivariate statistics in 14 skull and mandibular variables. There are significant differences in growth allometry across the 13 species - affecting their evolvability - the amount of morphological diversity or disparity that can be attained through selective breeding, which we quantifiy for some of the species investigate (dogs, cattle, and horses). Wolves-dogs and llamas-guanacos are the pairs that exhibit the greatest amount of change between the wild and the domestic form, domestic-wild pigs exhibit the least amount of differences. In spite of the statistical differences in the growth trajectory, there is little in the amount of change in Equus, Ovis, Camelus and Sus. The wild rabbit is characterised by a high proportion of allometric growth, making it a species with high potential for disparity. Skull variables showing the least amount of change are in the neurocranium (e.g., breadth of the braincase). The length of the nasals (LN) is the variable showing the greatest amount of change when all species are considered in the comparison between the wild and the domestic forms. Ongoing work on rates of evolution shows that these rates are lower in the process of domestication when compared to strong selection for particular breed traits. The differential patterns of change across species during domestication, also shown in life history traits (e.g., degree of variation in gestation length) show that using the silver fox experiment or the dog as models of domestication is of limited value, as canids exhibit within carnivorans and across mammals in general, a rather singular pattern in the changes associated with domestication.

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